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THE EFFECT OF TEMPERATURE AND SEASON ON DIGESTION AND UREA KINETICS IN GROWING WAPITI

by

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ROBERT WESTRA

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled

The Effect of Temperature and Season
on Digestion and Urea Kinetics
in Growing Wapiti

in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Animal Science.

ABSTRACT

The main objective of this study was to partition the effects of season (photoperiod and age) and temperature on growth, digestion and urea utilization in growing wapiti.

Eight 4-1/2 month old male wapiti were divided into two groups: one group exposed to a relatively constant temperature of 18-19 C (IN wapiti) and a second group exposed to outside ambient temperatures (OUT wapiti). Five experiments to measure the effect of season were conducted: one experiment per month of October, December, February, April and June. Photoperiod was by natural lighting. Growth rate during December, February and April was lower than that in October, whereas, in June the growth rate of the IN wapiti was similar to that in October. In June, the growth rate of the OUT wapiti changed little from the winter months. Growth rate was reduced when the wapiti were held in crates compared to being held in pens. Season had a significant effect on the following blood parameters: packed cell volume, white blood cell count, differential blood cell counts, plasma concentrations of calcium, inorganic phosphate and creatinine, and serum concentrations of thyroxine, and 3,5,3'-triiodothyronine; temperature had very little or no effect on these same parameters. Both season and temperature had a significant effect on serum alkaline phosphatase.

Dry matter (DM) intake/$w^{.75}$ (g/$w^{.75}$kg/d) dropped from 101.4 g/$w^{.75}$kg/d in October to 79.5 g/$w^{.75}$kg/d in December and remained relatively stable in February, April and June. Temperature had no effect on DM intake $w^{.75}$. Apparent digestibilities of DM, gross energy (E), nitrogen (N) and fat (ether extract) were significantly increased in

the winter and spring months compared to October. The digestibility of acid detergent fiber (ADF) was reduced markedly in December and February compared to October, April and June. Temperature reduced apparent digestibility of E, N, ADF and neutral detergent fiber (NDF). Mean retention time (MRT) of a ^{103}Ru label in the digestive tract was increased from 21.4 h in October to 28.7 h in February. Rumen and hind gut rate constants were also affected by season whereas temperature had little or no effect.

Plasma urea-N was increased from 20.2 mg% in October, to 25.2 mg% in December and remained relatively stable thereafter. Urea-N recycled decreased from 1.18 g/$w^{.75}$kg/d in October, to 0.47 g/$w^{.75}$kg/d in December and remained unchanged in the months that followed. Urea-N flux had a similar and parallel pattern as urea-N recycled. Season had no effect on urea-N excretion/$w^{.75}$ nor on urea-N clearance/$w^{.75}$. Less nitrogen was retained in December, February, April and June than in October, which reflected a depressed growth rate. Temperature had no effect on nitrogen retention and urea-N recycled to the digestive tract.

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CHAPTER 1

INTRODUCTION

Large ungulates are important to the viability and dynamics of many ecosystems (Odum, 1969; Moen, 1973). They have also been important resources for man for recreation purposes (Telfer and Scotter, 1975) but may, at the same time, be important resources for a greater efficiency in land use in some areas, through ranching of multi-species assemblages (Kimball, 1956; Dasmann, 1963; Nasinovich, 1970; Crawford, 1972; Telfer and Scotter, 1975). A strong information base on nutrition and bioenergetics of wild ungulates may provide a greater predictive capability within a given resource management system (Moen, 1973: Nelson and Leege, 1978).

Maloiy et al. (1968) suggested that nutritional factors which affect the nutritional status of wild animals could be classified into three general categories: 1) environmental factors, such as availability of food, water and minerals and exposure to various extremes of temperature and radiation; 2) behavioral factors, such as the activity of selecting food items; and 3) physiological factors, such as the manner and efficiency with which food is transformed into animal tissue. The environmental and behavioral factors can be, and have been, studied under field conditions. Physiological factors, in most cases, must be studied within a laboratory setting where the number of environmental and behavioral factors are more limited and controlled than under field conditions.

Studies have been designed to estimate nutrient requirements of wild ruminants (Mothershead et al., 1972; Lochman et al., 1973), to

study digestion and metabolism of various feedstuffs, (Silver et al., 1959; McEwan, 1970; Holter et al., 1975) and to assess nitrogen and urea utilization (Wales, 1972; Robbins et al., 1974; Kirkpatrick et al., 1975; Hove and Jacobsen, 1975). Several investigations have estimated seasonal effects of changes in body weight, growth rate and rate of feed intake in wapiti (Boll, 1958), in deer (Bandy et al., 1970; Holter et al., 1977) and in caribou (McEwan, 1968); and urea recycling in caribou (Wales and Milligan, 1972), in reindeer (Hyvarinen et al., 1975) and in deer (Robbins et al., 1974). However, few investigations have estimated the independent and/or the interacting effects of seasonal covariates such as temperature, photoperiod, wind, precipitation and age of animal on the utilization and efficiency of digestion of feedstuffs by cervids, and in particular, wapiti.

Changes in environmental temperature have been shown to alter digestion and metabolism in domestic ruminants (Westra, 1975; Christopherson, 1976) and to be indirectly related to metabolic activity in cervids (Silver et al., 1969), caribou and reindeer (McEwan, 1970). The effects of wind and precipitation are also known to contribute significantly to metabolic activity in ruminants (Ames and Insley, 1975; Moen, 1976). Furthermore it has been documented that the quality of feed consumed by deer appears to cause significant changes in feed intake (Ammann et al., 1973) in digestion and metabolism, and in nitrogen utilization (Maloiy et al., 1970; Robbins et al., 1974). Thus, changes in digestion by wild ruminants throughout any given year are probably largely a reflection of the quality and quantity (feed availability) of the herbage consumed. In addition to the environmental covariates, age of the animal is an important factor influencing

digestion and metabolism in growing animals with the relative size of the stomach reaching mature proportions by about eight weeks in sheep and goats, 3 - 4 mo. in deer, and 5 - 6 mo. in cattle (Church, 1973a). The effects of photoperiod on digestion and metabolic activity as an independent or interacting covariate of season has not been investigated in ruminants.

The objective of this study was to partition the effects of season and temperature on growth, digestive function and utilization of nitrogen by growing wapiti offered a ration of constant quality. Season, in the context of this theses, is understood to include only the covariates of age of the animal and photoperiod unless otherwise specified. Ambient temperature, although a covariate of season, was a partitioned effect and thus a fixed treatment variable. The effects of wind and precipitation were not influencing factors since all animals were sheltered in barns. This study also provided an opportunity to record data on early rearing, antler development and behavior of captive wapiti.

CHAPTER 2

REARING AND MANAGEMENT

The wapiti of this study, Cervus elaphus nelsoni (Banfield, 1977), belong to the same species as the red deer (Cervus elaphus elaphus) of Europe and Asia. However, mature wapiti are 2 to 4.5 times larger than the European red deer. Red deer are presently being studied intensively in Scotland (Blaxter et al., 1974) and in New Zealand (Drew and McDonald, 1977), as potential species for game ranching. Investigations on physiology, nutrition and behavior of red deer from infancy to maturity have been reported by a number of other researchers (Valler, 1970; Lincoln et al., 1972; Kyle, 1973; Guiness et al., 1974; Landholt, 1975).

Suggestions have been made that wapiti may be a valuable species for game ranching in North America (Anderson, 1951; Field et al., 1973; Telfer and Scotter, 1975), although very little has been reported on the rearing, training and domesticating of native wapiti.

The nutritive value of milk replacers fed to growing cervids, particularly wapiti, has also received little attention. Blaxter et al. (1974) reared red deer calves with moderate success on commercial ewe milk replacer fortified with vegetable oil to simulate the higher fat content in milk of red deer. Robbins and Moen (1975) compared the growth rate of white-tailed deer fawns reared by their dams with those artificially reared on evaporated milk reconstituted with casein and a vitamin-mineral mix. In spite of the rations offered, difficulties have been reported in hand rearing Odocoileine deer (Long et al., 1961; Silver, 1961; Buckland et al., 1975; Robbins and Moen, 1975), diarrhea

being one of the major causes of mortality (Kramer et al., 1971). Therefore several observations and measurements were made during the process of hand rearing the wapiti calves. In addition, an experiment was conducted to determine the digestibility of nutrients in two artificial milk replacers.

2.0.0. METHODS AND MATERIALS

The wapiti calves used in this study were obtained from two geographical sources.

Five wapiti calves were born at the University of Alberta Research Station. The dams of these calves had been trapped and trucked to the Station in Edmonton from the Ya Ha Tinda Ranch, on March 17 and 18, 1976. The elk were fed a ration consisting of brome-alfalfa hay ad libitum and approximately 5 kg of crushed oats daily from this time until they calved. Another ten wapiti calves were obtained from the State of Wyoming Game and Fish Commission, Sybille Research Station in June, 1976. By the end of June, two "Wyoming" calves died and two "University of Alberta" calves died, leaving eight males and three females (Table 3, Appendix 4). All calves from both groups of wapiti were born within one week of each other--between May 22 and June 1 (Table 3, Appendix 4). Similar birth dates for wapiti have been reported by Johnson (1951).

All calves were removed from their dams a few hours to four days following parturition. After being taken from the dams, the calves were then trained to drink from a beverage bottle fitted with a rubber nipple. Calves were given dairy cow colostrum for the first 2 to 3 days

Table 1. Guaranteed analysis of Supertreat[1] lamb milk replacer used to rear the wapiti calves.

Crude Protein	not less than 24.0 %
Crude Fat	not less than 30.0 %
Crude Fiber	not more than 0.5 %
Calcium	0.6 %
Phosphorus	0.7 %
Iron	0.002%
Zinc	0.005%
Vitamin A	not less than 7,040 I.U./kg
Vitamin D_3	not less than 1,584 I.U./kg
Vitamin E	not less than 8.8 I.U./kg

[1] Manufactured by Park City Products Ltd., Winnipeg, Manitoba. Oxytetracycline added at 100 g/11.4 kg Supertreat.

of life. Thereafter, a commercial lamb milk replacer, Supertreat (Table 1), was offered five times daily for the first 4-5 weeks and, subsequently, four times daily at 900, 1200, 1600 and 2000 h until the end of August. Supertreat was offered as a mixture of 20% by weight with water until the end of July, at which time the concentration was increased to 25%. Each calf was offered the amount of Supertreat it could tolerate without scouring. When the calves began to increase their forage and grain in intake, daily Supertreat feedings were successively reduced, on a body weight basis, to the time of weaning.

Supertreat initially was warmed to 37-40 C, but when the calves reached 3 to 4 weeks old, the milk rations were offered at refrigerator temperature (2-4 C). No digestive upsets resulted. Young of both domestic cattle (Walker, 1950) and sheep (Penning et al., 1977) have been successfully raised on cold milk.

The energy content of Supertreat on a DM basis was determined by bomb calorimetry to be 18.6 kJ/g. The calculated daily allowance for calves between 3 and 50 days of age was from 250 to 315 kJ/kg of body weight (13.4 to 16.9 g/kg). A maximum Supertreat energy consumption (ca. 315 kJ/kg/d) was reached between 20 and 40 days of age. Le Du et al. (1976) recorded similar observations in bovine calves.

By the end of September, 1976, the wapiti calves were consuming the pelleted ration described in Table 2. After October the calves were maintained solely on this ration to the end of June, 1977. The average energy and protein content of the ration was, respectively, 17.8 kJ/g and 17.2% (Table 3). Water and cobalt-iodized, block salt were always available. Water offered to the outside animals was heated to approximately 3-5 C with electric coils fitted near the bottom of plastic

Table 2. Constituents of the pelleted ration offered to growing wapiti, from September, 1976, to June, 1977.

Composition (dry matter basis)*	%
Alfalfa (minimum 15% protein)	25.5
Barley	31.0
Wheat bran	14.0
Beet pulp	13.5
Molasses, beet	7.0
Soybean meal	8.5
Salt (trace mineralized)	0.5
Vitamin A, D and E*	0.04
	100.0

*Containing 9,988,000 I.U. of vitamin A. 1,248,500 I.U. of vitamin D_3 89,188 I.U. of vitamin E per kg.

Table 3. Chemical components of the pelleted ration.

Gross Energy (kJ/g)	17.8
Crude Protein (%)	17.2
Neutral Detergent Fiber (%)	47.9
Acid Detergent Fiber (%)	19.3
Ether Extract (%)	2.00
Calcium (%)	1.11
Phosphorus (%)	0.46
Moisture (%)	10.4

pails (14 litres).

Beginning in October, the wapiti were held in individual pens about 1.2 x 2.4 m. Wood shavings were used for bedding, except during the digestibility trials, when rubber mats were used to prevent slipping. Wood shavings absorbed urine fairly quickly and would not provide as many nutrients as straw if eaten. It was found that dryness was important; since, whenever the hoof and body surfaces came in contact with a wet floor, they soon became infected.

Adjustable rope head-halters were always used to transfer animals from one location to another. Wapiti 1139 consistently refused to be led. The other calves responded to leading when patience and firmness were exercised. Forcefulness was met with considerable resistance and retaliation.

2.1.0. REARING OBSERVATIONS

Training the wapiti calves to suckle from a bottle met with considerable resistance. Four animals resisted all efforts to encourage suckling and subsequently died one to two weeks after birth. After these unsuccessful training attempts, two other calves were force-fed by stomach tube four times daily for 4 to 6 weeks. The stomach tube consisted of a soft polyethylene tubing (10 mm ID) about 1 m long. One end of the stomach tube was inserted into the back of the mouth to initiate the swallowing reflex so that about half the length was swallowed by the calf. The opposite end of the stomach tube had a funnel affixed

for administering the milk ration. After several days, the two calves (#1135 and 1139) accepted the stomach tube with little resistance.

It soon became apparent that accepting milk from an artificial source appeared to be related to taste, rather than to such factors as fear, inability to suckle or, possibly imprinting. When the two animals reared with a stomach tube were offered commercial milk (containing 394 ml of Alpha evaporated milk and one litre of Palm homogenized whole milk) 3-4 weeks after they were born, they soon began to suckle from a nursing bottle and the stomach tube became unnecessary. However, when these animals were again offered Supertreat, they immediately refused to suckle. Starvation was not a sufficient stimulus to force them to suckle Supertreat. The wapiti that were offered the milk rations during the digestion trial also refused to accept Supertreat afterwards and they always tasted the ration before suckling. If the bottles contained milk, bottles containing Supertreat could be quickly substituted. When the wapiti became conscious of the taste, Supertreat was then unaccepted. These observations suggested that the early training of wapiti to suckle, especially the wapiti fed by stomach-tube, may be related to taste. Stephens (1974) observed, however, that young bovids were unable to associate suckling with feeding after what he defined as the "receptive" period. The two animals refusing to suckle Supertreat were still able to associate suckling with feeding up to one month of age, since they readily accepted the milk after this period of time. Therefore, the unacceptability of Supertreat was interpreted to be associated with a strong aversion to its taste by the wapiti.

When the calves were together as one group, sucking the prepuce, scrotum and other body surfaces often occurred. Stephens (1974)

suggested that this activity in bovine calves may arise from deprived oral activity as a result of milk being quickly consumed from a nursing bottle. Lorenz (1950) explains this activity by the 'psychohydraulic model', that is, there is a drive within the animal to perform a specific activity even though the factors needed to trigger it are absent.

Soon after the adjustment to people, many of the calves displayed the preorbital gland by opening it wide just prior to feeding, during feeding, when the researcher groomed the calf, or when the calf urinated. Whenever the calves were aroused, or haltered in preparation of going out-of-doors, many of them also displayed their preorbital gland. This phenomenon was most often observed in wapiti 1135, 1138 and 1128; the same animals which showed signs of imprinting on specific people. This behavioral characteristic has been discussed by Muller-Schwarze (1975) and appears to be associated with pleasant and satisfying experiences.

Some animals associated with one person more than another. This was obvious with wapiti 1135 and especially with wapiti 1138. This behavior may have been related to the early association of the reseacher and the newly born calf (Gilbert, 1971; Fraser, 1976). Wapiti 1138 would often attempt to escape, strike, or bite the person against whom it had a great dislike. This behavior also has been reported in roe deer (Capreolus capreolus) (Prior, 1968, p. 102).

Social bonding was observed between animals occupying pens adjacent to each other. This behavior became evident whenever an animal was removed, or whenever the animals were rearranged between pens. Shrill cries were heard and attempts were made to leap from one pen to another and return to the original arrangement. When the wapiti were together in one large pen as a group, the animals that exhibited a strong social

removed, or whenever the animals were rearranged between pens. Shrill cries were heard and attempts were made to leap from one pen to another to return to the original arrangement. When the wapiti were together in one large pen as a group, the animals that exhibited a strong social bond tended to stay together. Fraser (1976) in his review, reported that when bonding was prevented between individuals in domestic calves and pigs, growth rates and resistance to disease diminished markedly.

Wapiti 1136 had the occasional habit of grinding its teeth. It may have been associated with dominance, since this animal quickly assumed dominance in the herd whenever they were together as a group. This behavior has been observed as a sign of dominance in Muntjac deer (_Muntiacus reevesi_) (Barrette, 1977).

The wapiti were often observed eating wood shavings. When the wood shavings were removed during experiments, the animals chewed the wooden pen dividers and licked and chewed their plastic water pails. Wires or materials inadvertently left beside the pens were chewed and sometimes eaten. When the wapiti were in metabolic crates similar chewing activities were observed. At first this behavior was believed to be a symptom of phosphorus deficiency (pica), but they showed no interest in a mixture of salt and dicalcium phosphate. Similar behavior patterns were reported by other workers in domestic ruminants (MacFarlane, 1974; Dantzer and Baldwin, 1974), and in captured wild wapiti (Boll, 1958). Bubenik and Casnocha (1963) observed increased browsing behavior in red deer when feeding periodicities were altered, suggesting that increased bark peeling may be stress induced. Ilan _et al._, (1973) reported that calves kept in pens spent 19% more time eating, 11% more time ruminating

and 11% less time jumping than calves not in pens. Other investigators (see review by Dantzer, 1977) suggested that the chewing and licking behavior observed in the wapiti may be a displacement activity or a redirected activity resulting from the physical constraint of the pens. This activity was especially noticed whenever a person cleaned out or walked near a pen, when attempts often were made by the wapiti to bite, chew or lick the clothing of that person.

2.2.0. DIGESTION OF MILK RATIONS

An experiment was designed to compare the apparent digestibilities of dry matter (DM), gross energy (E), nitrogen (N) and ether extract (fat) between Supertreat and a ration consisting of a mixture of 394 ml of Alpha evaporated milk and 1 liter of Palm homogenized milk (milk). Methods and materials used in this experiment are described in Appendix 4. Supertreat was chosen for the similarity of fat percentage to cervid milk (reviewed by Robbins, 1973) and for its commercial availability. The experiment was conducted between July 3 and July 7, 1976.

Gross energy contents of both rations were the same (18.6 kJ/g DM). The N and fat content was 3.8 and 28.6% respectively for Supertreat and 4.8 and 2.15% respectively for milk (DM basis). The significantly lower ($P<0.01$) DM intake of milk appeared to be related to the greater apparent digestibility of fat and not DM and E (Table 4). The higher apparent digestibility of fat and N in the milk-fed wapiti may have been due to the 17% reduction in DM intake which caused an increased potential for digestion in the gut (Penning et al., 1977). Fewer inci-

Table 4. The mean apparent digestibilities of dry matter (DM), gross energy (E), nitrogen (N), and ether extract (fat); and the mean retention time (MRT) of digesta in wapiti offered either Supertreat or milk.

Milk Ration	Intake	Apparent Digestibility (%)				MRT
	$(g/w^{.75}kg/d)$	DM	E	N	fat	(h)
Supertreat	37.6*	91.4	93.2	84.4*	97.4*	33.2
Milk	31.1	93.0	94.4	90.4	99.0	34.6

*Significantly different between treatments (P<0.01). Student's t-test.

dences of diarrhea were recorded in the wapiti receiving milk than in the wapiti receiving *Supertreat*, which may have been related to an improved N digestion and the reduced amount of DM consumed (Penning *et al.*, 1977). Mean retention times (MRT) of digesta in the digestive tract of the calves estimated by using the radioactive label ^{103}Ru (Appendix 4) were similar between treatments. The large variability in the MRT's between wapiti may have been the result of different levels of intestinal adjustment to roughage and rolled oats which the calves were beginning to consume prior to the experiment (Ruckebusch and Bueno, 1973).

2.3.0. DISEASES AND DISORDERS

A very resistant *Escherichia coli* infection emerged in late July to early August which manifested itself as a severe diarrhea. The *E. coli* was sensitive only to choloramphenicol, furacin and gentamycin. Strict hygienic procedures such as cleaning and disinfecting the pens with a creosote-base disinfectant, the use of a boot disinfectant bath before entering the general area and the sterilization of nursing bottles after every feeding were enforced. Whenever diarrhea became severe, *Supertreat* or milk was withheld for one to four feedings. Oral therapy of electrolytes and glucose was administered similar to that described by Radostits (1975), to maintain hydration.

Wapiti 1137 fractured its right front leg June 29, 1976, when attempting to leap over a fence. The leg was set in a plaster cast after anesthetizing the animal with Rompun (xylazine hydrochloride). The leg successfully healed in 6 weeks. Wapiti 1128 suffered from an

umbilical hernia which was surgically repaired August 17, 1976. Fluids leaked through a small fenestra in the peritoneum, left by the wound, which occasionally became a small edematous swelling. Wapiti 1133 severly twisted its right hind leg by slipping on some ice in October when being led from one barn to another. The unjury was diagnosed to be in the femur-sacrum joint. Thereafter, wapiti 1133 walked by swinging this leg outward and then forward.

Two IN wapiti (one from Wyoming and one from the University of Alberta) within the same unit died (February 17 and 19) of what was tentatively identified, in autopsy, as malignant catarrhal fever (MCF). No virus was isolated from either animal, thus, positive identification of the problem was not made; however, many of the clinical signs and histopathological features resembled those of MCF (Clark et al., 1970; Wyand et al., 1971; Wobeser, et al., 1973; Rweyemau et al., 1976; Ohshima et al., 1977). Three to four days before death, the animals went off feed and drank very little water. Rectal temperatures remained normal (38.9C) until death. Rumen and gut motility became static soon after feed intake ceased. Twenty-four hours before death the animals became diarrhetic. Twelve hours later rectal hemorrhaging and large losses of blood occurred. Antibiotics and electrolyte therapy were to no avail. It was believed that the two wapiti, which shared common water bowls, contacted the virus through direct nasal contact with a sheep occupying an adjacent pen. Transmission of MCF to cattle by sheep showing no signs of having the disease has been suggested by several authors (Pierson et al., 1974; Storz et al., 1976). Cervids appear to have very little or no resistance to the disease (Wyand et al., 1971).

All animals were free of pathological internal parasites as determined by fecal counts using a flotation technique (Levine *et al.*, 1960).

CHAPTER 3

EXPERIMENTAL DESIGN AND ENVIRONMENTAL CONDITIONS

In October, 1976, the first of five major experiments was started to determine the effects of season and temperature on growing wapiti calves. Eight male wapiti were available from October, 1976, to June, 1977. Three female wapiti were also available, but were only included in the discussion on growth. The experimental designs used in this study are shown in Figure 1. The eight male wapiti were divided into two equal groups. One group was kept inside a barn (IN wapiti) and exposed to a relatively constant temperature. The second group was kept in a shed open on the south and exposed to outside ambient temperatures (OUT wapiti).

Five experimental periods (1 through 5) were used to represent the following seasons:

1. Mid-Autumn: October 17-24 and October 27 - November 3, 1976
2. Winter Solstice: December 13-19 and December 22-29, 1976
3. Mid-Winter: February 6-13 and February 16-23, 1977
4. Early Spring: April 12-21 and April 25 - May 4, 1977
5. Summer Solstice: May 24 - June 3 and June 6-16, 1977

Since only two double metabolic crates (Appendix 1) were available, the wapiti within each temperature treatment were divided into units consisting of two wapiti per unit. Thus, the wapiti in unit 1 occupied a crate during week 1, and the wapiti in unit 2 during week 2. This design, illustrated in Figure 1 as model A, estimated the fixed effects of temperature and season, the random effects of animals and units,

MODEL A: Allocation of animals to units

	IN wapiti		OUT wapiti	
	Unit 1	Unit 2	Unit 1	Unit 2
Experiment 1	1135*	1133	1134	1128
	1139	1137	1136	1138
Experiment 2	1135	1133	1134	1128
	1139	1137	1136	1138
Experiment 3	1135	1133	1134	1128
	1139	1137	1136	1138
Experiment 4	1133	–	1134	1128
	1137	–	1136	1138
Experiment 5	1133	–	1134	1128
	1137	–	1136	1138

*Animal

MODEL B: Allocation of units to crates and pens

		IN wapiti		OUT wapiti	
	Week	Crate	Pen	Crate	Pen
Experiment 1	1	Unit 1	Unit 2	Unit 1	Unit 2
	2	Unit 2	Unit 1	Unit 2	Unit 1
Experiment 2	1	Unit 1	Unit 2	Unit 1	Unit 2
	2	Unit 2	Unit 1	Unit 2	Unit 1
Experiment 3	1	Unit 1	Unit 2	Unit 1	Unit 2
	2	Unit 2	–	Unit 2	Unit 1
Experiment 4	1	Unit 2	–	Unit 1	Unit 2
	2	–	Unit 2	Unit 2	Unit 1
Experiment 5	1	Unit 2	–	Unit 1	Unit 2
	2	–	Unit 2	Unit 2	Unit 1

Figure 1. Experimental designs

and the related interactions. The effects of units and weeks were not separated in this design.

The effect of week 1 and 2, and of holding the wapiti in crates on feed intake and apparent digestibility (hereafter called digestibility) was tested by the design shown in Figure 1, as model B. Thus, in week 1, the wapiti in unit 1 were held in crates, and the wapiti in unit 2 in pens; whereas, in week 2, the wapiti in unit 1 were held in pens, and the wapiti in unit 2 in crates. The fixed and random effects tested in model A were again tested in model B. The equations for models A & B are shown in Appendix 2. The analyses of variance for all parameters determined are shown in Appendix 5. Differences between adjusted mean values were calculated using Duncan's New Multiple Range Test (Steel and Torrie, 1960). The mean values calculated for the fixed and random effects were adjusted for the missing values in April and June, 1977, by using a least squares algorithm (Dixon, 1973).

The IN wapiti were exposed to a relatively constant temperature of 18.6 ± 3.3 C from October, 1976, to March, 1977, and 19.8 ± 2.4 C from April to June, 1977. The lowest outside ambient temperatures occurred during December (Table 5), just prior to experiment 2, and in January, soon after experiment 2 (Figure 2). Following the period of the lowest temperature of the year (January), mean ambient temperatures increased to levels above freezing, except for a short period in mid-March. Thereafter, mean ambient temperatures increased to highs in late April and June of 14 C.

Photoperiod was by natural lighting via windows for the IN wapiti, and via the open side of the shed for the OUT wapiti. Average light intensity measurements were made at wapiti-eye-level inside a

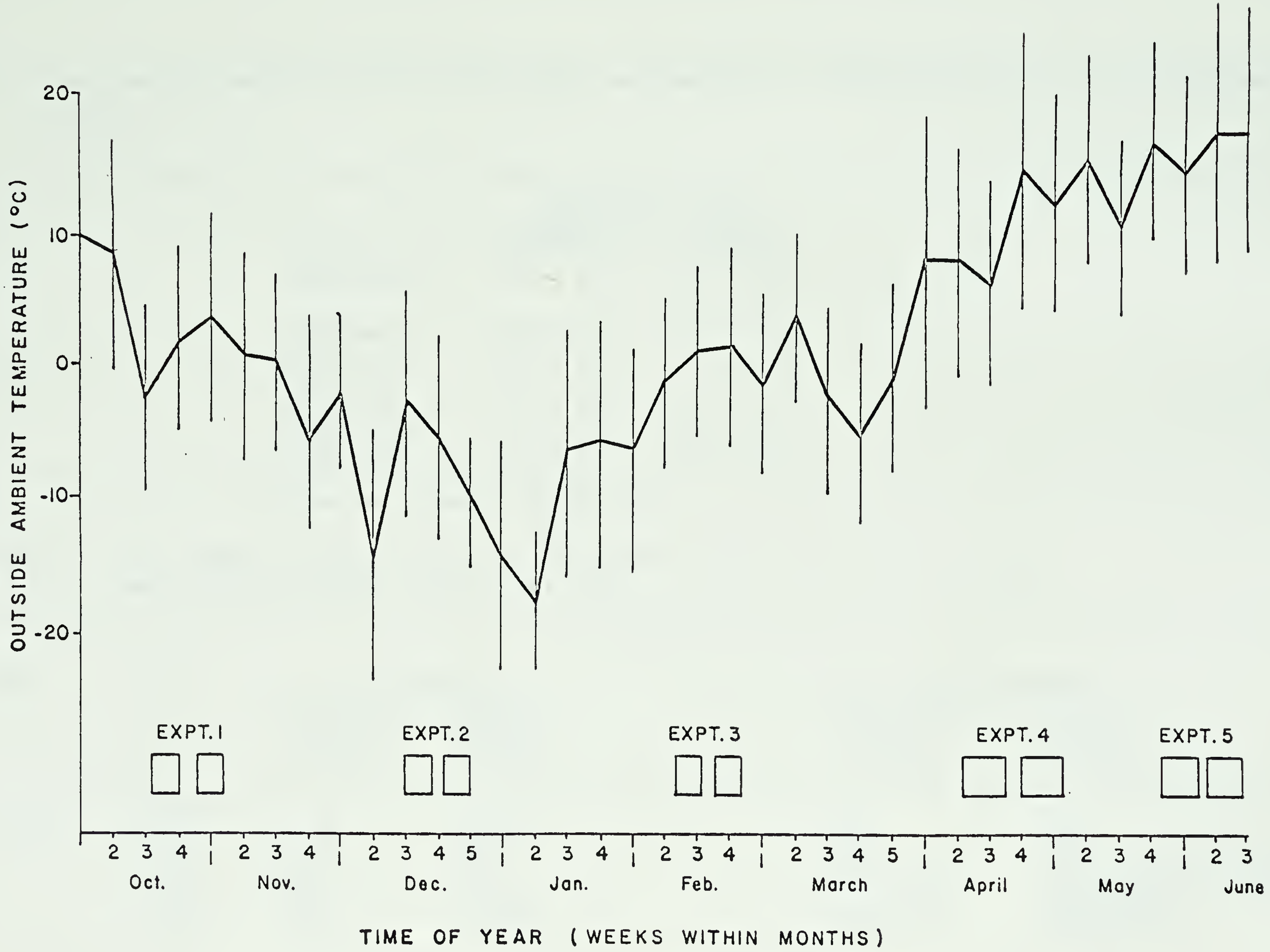

Figure 2. Average ambient temperatures (7 d averages) of the outside temperature treatment. Vertical lines represent ± S.D. The five experimental periods are shown as open blocks.

Table 5. Mean ambient temperatures the OUT wapiti were exposed to during the week of each experimental period.

	Temperature (C)	
	Week 1	Week 2
Experiment 1	2.2 ± 6.7[1]	4.2 ± 2.2
Experiment 2	-3.0 ± 6.3	-5.6 ± 7.1
Experiment 3	-0.8 ± 5.8	2.2 ± 7.3
Experiment 4	6.2 ± 8.3	14.0 ± 9.1
Experiment 5	14.4 ± 7.7	17.3 ± 9.8

[1] mean and standard deviation

Table 6. The amount of light the IN and OUT wapiti were exposed to on a cloudless and an overcast day in May, 1977.

Day	Time	IN TREATMENT		OUT TREATMENT		
	(h)	Horizontal reading (luxes)	Vertical reading (luxes)	Horizontal reading (luxes)	Vertical reading (luxes)	
May 25	0730	54	107-215	377	1291	cloudless day
	1030	22-32	140	1076	4300	
	1330	22-32	43-86	1076-6450	2150-10760	
	1530	22-32	108-323	1076-6450	2150-8600	
	1930	5-22	5-22	215-1610	538-2150	
May 28	1200	5-22	5-22	108-1184	322-1184	overcast & raining
	1500	5-22	10-32	108-538	538-1076	

representative pen of both barns using a Parlux electronic luxmeter (Gosan GMBH, Erlangen, Germany). Readings were obtained for cloudless and overcast days. The IN wapiti were adjacent to a row of west-facing windows approximately one m^2 and spaced in 1 m intervals. Unfortunately, the amount of illumination within a given pen was different between temperature treatments. Illumination inside the pens of the IN treatment were 100 to 800 luxes lower than inside the pens of the OUT treatment (see Table 6). At night, during November and December, the IN wapiti were exposed to a low intensity light that reflected off a distant wall, the source, of which, arose from another section of the barn.

All animals were housed individually (pen sizes were about 1.2 by 2.4 m) during all periods except for 10- to 14-day periods, in which intensive measurements were made. Water was continuously available in 14 liter pails and feed was provided *ad libitum*, once daily.

Crates were constructed basically as described by Cowan *et al*., (1969). They were initially designed for deer (Appendix 1a). Larger crates were necessary for experiments 4 and 5 (Appendix 1b). They were approximately 3'2" (112 x 244 cm) in area , and the sides were 6' (183 cm) high. The steel floor grid was constructed of flat 1/4" x 1 1/2" steel which was set on edge leaving 2" (61 cm) spaces between each grid plate. The fecal and urine collecting tray was modified (Appendix 1c) and attached to the frame of the crate, with a slope of approximately 2 cm in 1 m, so that the urine would run quickly into the collecting bucket beneath. Urine was collected in pails containing a 25 to 50% sulfuric acid solution, depending on the volume of urine excreted. The urine collected, contained no more than a maximum of 4% sulfuric acid by volume of urine excreted, at any one time.

The wapiti kept in the pens were provided rubber mats that covered about 90% of the cement floor surface. The floors were sufficiently sloped so that the urine drained away. Fecal material was scraped from the rubber mats and cement surfaces once a day.

CHAPTER 4

EFFECT OF SEASON AND TEMPERATURE ON GROWTH

Little or no information is available on the effect of season and temperature on the rate of growth in wapiti. Blood and Lovaas (1966) reported that body weights of slaughtered Manitoba wapiti ranged from 134 kg in a five month old male to 478 kg in an eight year old male. Flook (1970), citing Greer and Howe (1964), reported that the wapiti in Yellowstone National Park appeared to reach their asymptotic weight between the ages of three and seven years. Body weights of wapiti slaughtered at various ages have been studied by Flook (1970) and Field and Hepworth (1974). Flook (1970) reported that the mean body weight for mature males and females was ca. 333 kg and 259 kg , respectively.

Wapiti exhibit a cyclic body weight response to season, similar to other cervid species (McEwan, 1977). Boll (1958) studied the responses of captive wapiti to various winter diets and observed a 10 to 17% body weight loss over the winter season. Dean *et al*., (1976) found that 62% of the calves still gained weight during December through March, while 22% lost weight. Furthermore, nearly 47% of the adult females gained weight, while 47% lost weight during this same period.

In this study, body weights of the wapiti were periodically taken to study the effect of season and temperature on growth.

4.0.0. METHODS AND MATERIALS

The wapiti were weighed soon after birth and then every two to five days to the first 100 days. Food and water were not removed before weighing. Body weights were taken less frequently after 100 days, and between experiments, but on a regular basis during the experiments. Three females were included for comparison with the eight males. Individual body weights are recorded in Table 2, Appendix 4. Theoretical von Bertalanffy equations (Brown _et al._, 1977) were fitted using with a computer program (Dixon, 1973) which calculated the three coefficients to describe the relationship of growth and age. The equation is described as follows:

$$G_t = A(1-be^{-kt})^3$$

where G = body weight (kg) at age t.

A = asymptotic body weight the animal can attain at maturity.

b = a scaling parameter (constant of integration) which is established by the initial values of body weight (w_o) and t. ($w_o \neq 0$ or $t_o \neq 0$)

t = age of animal in days.

k = maturing index; decline in growth rate.

4.1.0. RESULTS AND DISCUSSION

The wapiti calves had a mean birth weight of 14.5 kg and gained an average of 0.33 kg/d (range = 0.16 to 0.48 kg/d) in the first 100 days following birth. Dean et al. (1976) and Thorne et al. (1976) reported average birth weights of 16.0 and 16.9 kg, respectively, in wapiti; while Johnson (1951) reported a mean birth weight of 14.5 kg. Johnson (1951) reported that the males tended to be 2 kg heavier than the females. He calculated the average daily gain of wapiti from 2 to 14 days old to be 0.91 kg. A calf reared on domestic cow's milk gained 0.45 kg/d.

Most calves in this study lost weight (1 to 2 kg) following birth (Figures 3a, 3b, and 3c), as a result of the difficulties in training the animals to suckle Supertreat. Wapiti 1137 had the greatest rate of gain (0.55kg/d, after July 1), while wapiti 1139 had the lowest rate of gain (0.18 kg/d, after July 1). The lower growth rates of wapiti 1135 and 1139 may have been due to the stress of feeding them daily with a stomach tube. Doyle et al. (1977) demonstrated that audiogenic stress reduced growth in bone length and mass per unit length in laboratory rats. Stress syndromes due to the reduced pen size of pigs and the prevention of social bonding between mates of calves and pigs pigs were shown to depress growth rate (Lanneck et al., 1974). The wapiti that best adjusted to pens, to people and to routine activities also appeared to have the least digestive problems and the greatest growth rates, for example, wapiti 1136 and 1137.

The growth pattern of wapiti 1137 (Figure 3b) showed a period of increased growth rate between 300 and 350 d. The growth rate of wapiti

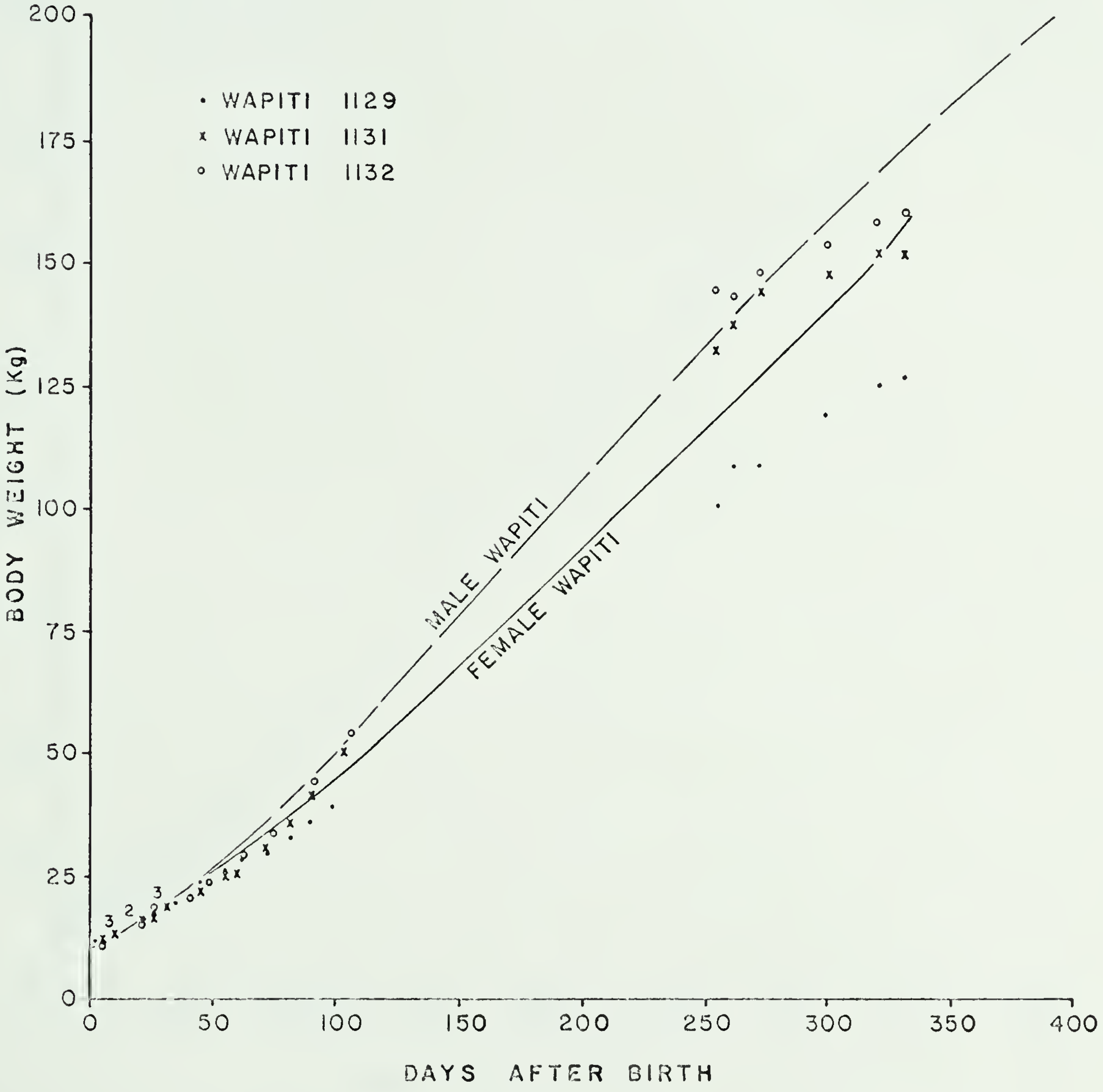

Figure 3a. Growth curve of male and female wapiti.
The von Bertanlanffy relationship describing the curve for females is $G_t = 331 (1 - 0.686e^{-0.00347t})^3$ kg and for males is $G_t = 313 (1 - 0.686e^{-0.005151t})^3$ kg; where, t = days and G_t = body weight (kg) at time t.

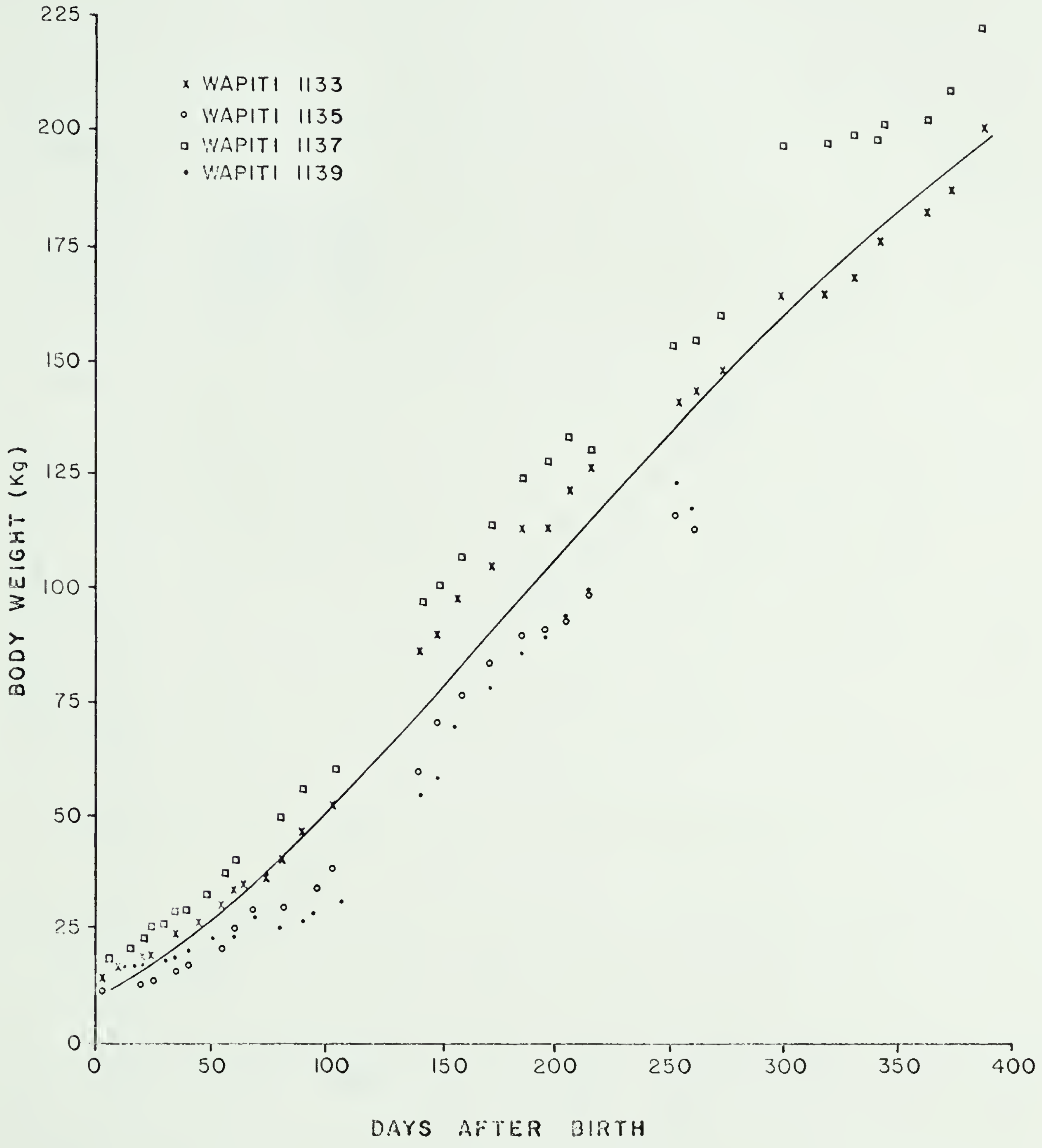

Figure 3b. Growth curve of IN wapiti.
The von Bertanlanffy relationship describing the curve is
$G_t = 313 (1 - 0.686e^{-0.005151t})^3$ kg; where, t = days and
G_t = body weight (kg) at time t.

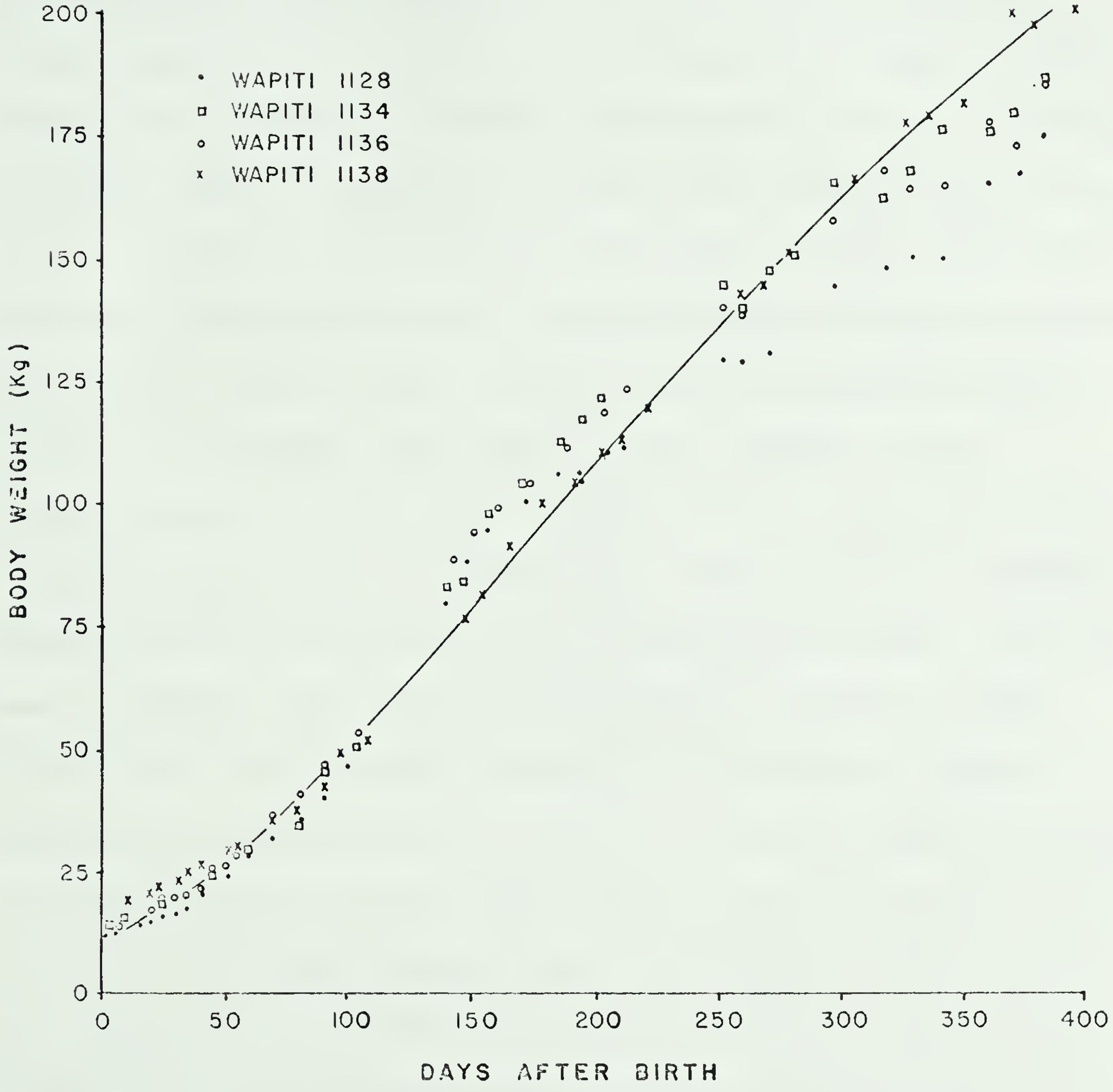

Figure 3c. Growth curve of OUT wapiti.
The von Bertanlanffy relationship describing the curve is
$G_t = 313\ (1 - 0.686e^{-0.005151t})^3$ kg; where, t = days and
G_t = body weight (kg) at time t.

1133 (Figure 3b) also showed an increase during this period, but not as dramatic as that of wapiti 1137. The rate of growth of the OUT wapiti was cyclic and tended to decrease with time between the period of 300 and 350 d (Figure 3c). One reason for observing an increased rate of growth in the IN wapiti during April and June and not in the OUT wapiti (Table 7) may be related to the differences in light intensity between the two groups. Aschoff's rule states in part that reduced light intensity leads to a reduction in length of the circadian cycle (τ)[e.g. τ(day) > τ(night); Quay, 1968; Daan and Aschoff, 1975]. Thus, the IN wapiti may have been responding to a spring-summer photoperiod earlier in the year than the OUT wapiti. Weight accertion in cervids normally occurs in mid-summer and weight stasis normally occurs during the winter in wild cervids (McEwan, 1977). The wapiti in this study generally grew at a constant rate, although periods of decreased growth rate often occurred during the digestibility trials. In the first week of February, the rate of growth decreased in both IN and OUT wapiti (0.178 and 0.136 kg/d, respectively) for which no apparent explanation could be offered. Greer and Howe (1964) observed in wapiti yearlings a 3% loss in body weight between December and January, and a 7% loss in body weight between January and February. These estimates were based on hunter dressed carcasses. Boll (1958) reported weight losses of up to 17% in wapiti calves fed hay and browse during the winter season, whereas Hungerford (1952) reported a weight stasis in calves fed an unrestricted ration during the winter period. The general growth rate pattern during the winter observed in the wapiti of this study was similar to that reported in red deer (Ryder, 1977), in the odocoileine species (Wood, et al., 1962; Bandy et al., 1970), and

Table 7. Mean daily rates of body weight gain by wapiti calves within weeks of each experiment and temperature treatment.

	Rates of Body Weight Gain (kg/d)					
	IN Wapiti			OUT Wapiti		
	Week 1	Week 2	Mean[1]	Week 1	Week 2	Mean
Experiment 1	0.540	0.784	0.662^{a}[2] (0.09)[3]	0.825	0.856	0.841^{a} (0.09)
Experiment 2	0.670	0.219	0.444^{ab} (0.09)	0.505	0.411	0.458^{ab} (0.09)
Experiment 3	−0.287	0.477	0.178^{b} (0.09)	−0.184	0.456	0.136^{b} (0.09)
Experiment 4	0.250	0.488	0.401^{ab} (0.16)	0.0170	0.263	0.217^{b} (0.09)
Experiment 5	0.525	0.010	0.801^{a} (0.16)	0.080	0.488	0.284^{b} (0.09)

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[1] The mean body weight gain within the temperature treatment of each experiment.

[2] When subscripts differ within columns the values are significantly different from each other ($P<0.01$). Duncan's New Multiple Range Test.

[3] Numbers within brackets are standard errors of the mean.

in caribou (McEwan, 1968), a characteristic which may have been related to feed quality. This will be discussed more fully in chapter 8.

There was a significant crate effect ($P<0.05$) on body weight gain. When the wapiti were in crates they had an overall mean body weight gain of 0.337 kg/d, whereas the animals in pens had an overall mean of 0.547 kg/d.

The theoretical von Bertalanffy equation of best fit for describing growth with age for males was:

$$G_{t(m)} = 313(1 - 0.686\ e^{-0.005151t})^{3}\ \text{kg} \qquad (1)$$

$$\text{S.E.} = 8.99$$

and for females was:

$$G_{t}(f) = 331(1 - 0.686\ e^{-0.00347t})^{3}\ \text{kg} \qquad (2)$$

$$\text{S.E.} = 6.22$$

Von Bertalanffy equations have been used to describe growth in domestic and tropical ruminants (Brown et al., 1977; Howells and Hanks, 1975; Hanks et al., 1976). Growth in wapiti as described by the von Bertalanffy equation, tended to underestimate birth weight, overestimate the mature weight of the three females and estimate reasonably well the mature weight in the males. The predicted mature weight of males was 313 kg. Wapiti 1139 had a slow growth rate which was due largely to the stress of feeding it by stomach tube and a predicted

mature weight of 700 kg was calculated. When wapiti 1139 was not included in the analysis, a predicted mature weight of 290 kg was obtained. The von Bertalanffy estimates of mature weight tended to underestimate the mature weight of males when compared to body weights of mature male wapiti ranging from 300 to 375 kg reported by Greer and Howe (1964), Blood and Lovaas (1966) and Flook (1970). However, when the predicted mature body weights of the wapiti of this study were compared to the body weights reported by Dean *et al*. (1976) the predicted mature body weight may have been overestimated. Dean *et al*. (1976) reported body weights of wapiti only up to 2 years old, and they ranged from 193 to 212 kg, 30 to 50 kg less than those of comparable ages reported by Flook (1970). The average mature weight of the three females (331 kg) in this study were about 70 kg greater than the average values reported by Flook (1970), and about 100 to 110 kg greater than those reported by Dean *et al*. (1976). However, the body weights of wapiti 1131 and 1132 are more closely related to the curve predicted for the male wapiti than for the female wapiti (Figure 3a). The growth rate of wapiti 1129 was greatly reduced compared to the other female and male wapiti, and largely contributed to overestimating the predicted mature body weight.

Estimated k values using Brody's model for describing growth have been derived in deer, *Odocoileus spp*. (Wood *et al*., 1962; Bandy *et al*., 1970), in reindeer (*Rangifer tarandus*)(Krebs and Cowan, 1962), and in caribou *Rangifer tarandus groenlandicus* (McEwan, 1968). The k values estimated in wapiti derived by the von Bertalanffy equation were 0.005151 for males and 0.00347 for females and were greater than those reported for reindeer (0.001429 to 0.003398) (McEwan, 1968) and for

blacktailed deer (0.001919) (Bandy et al., 1970) and smaller than those reported for mule deer (0.010 - 0.018) (Wood and Cowan, 1962). However, the k values estimated by the model of Brody are reported to be smaller than those estimated by von Bertalanffy (Brown et al., 1977). According to the hypothesis based on different breeds of cattle (Fitzhugh, 1977; Brown et al., 1977) a small k value when compared to a large k indicates that animals grow slower, reach a point of inflection earlier, have a longer maturity interval, and reach a larger body size. The differences of k values between wapiti sexes did not support the above hypothesis. The male wapiti had a larger k value than the females (compare k values in equation 1 and 2). According to Flook (1970) and others (Greer and Howes, 1964; Dean et al., 1976) male wapiti reach their adult weight about two years later than the females and are on the average 75 kg larger in body weight. More wapiti body weight data will be required for a more complete analysis in testing the von Bertalanffy growth curve hypothesis.

CHAPTER 5

EFFECT OF SEASON AND TEMPERATURE ON ANTLER DEVELOPMENT

Antlers are bony structures arising from the frontal bones of most members of the deer family (Cervidae). Antlers are usually restricted to the male species. Before, or soon after birth, depending on the species (reviewed by Chapman, 1975), pedicles grow out of the skull. They are covered with skin and soft hair and form the base upon which antlers develop and are later cast. Antlers are composed of bone and grow rapidly from the tip outward. Growth usually begins in late winter—early spring. During the growth phase, velvet covers the antler to protect it and provide a framework for the circulatory system. Velvet is an extension of normal skin from the head, but usually much thicker. In early autumn, when the antler matures, the velvet dies and is subsequently shed in preparation for the rutting season.

The circannual growth and casting of antlers has been shown to be regulated by several pituitary hormones and testosterone. This has been demonstrated in white-tailed deer (*Odocoileus virginianus*)(Wislocki *et al*., 1947), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and other antler bearing ruminants (Chapman, 1975). Whitehead and West (1977) and Whitehead and McEwan (1973) have demonstrated in caribou and reindeer (*Rangifer tarandus spp.*) and Bubenik *et al*. (1975) in white-tailed deer that plasma testosterone concentrations are cyclic. Testosterone levels peak between September and November, and remain at or near undetectable levels for the remainder of the year. Castration not

only inhibits testosterone production, but in deer leads to a continuous growth of antlers (Wislocki et al., 1947). When testosterone was administered to a castrate in these studies a subsequent shedding of the velvet occurred. This was soon followed by the antlers being cast as the levels of testosterone fell to zero (Wislocki et al., 1947; Lincoln et al., 1972; West and Nordan, 1976).

The daily light-dark cycle has been shown to be a powerful Zeitgeber (entrainment agent) for pituitary hormone production via the pineal gland in rodents (Thibault et al., 1966). Whether the pineal gland in ruminants regulates testosterone via the pituatary releasing factors similar to that in rodents (Quay, 1970), is not certain yet; although indirect evidence indicates that it may. Goss (1977) has shown that sika deer (Cervus nippon) will retain their antlers when exposed to light cycles of 12 hours of light and 12 hours of dark, but will soon cast their antlers when exposed to a light regime of 13 hours of light and 11 hours of dark. That is, as daylight hours increase beyond 12 h, antlers are cast and new ones are grown which corresponds to that observed in adult wapiti. Wapiti normally lose their antlers in March and April (Brown, 1971) when daylight hours are increasing.

It has been suggested that cold temperature reduces the intensity of sexual activity during the rut (Darling, 1963), as well as, affecting the time of antler casting in red deer in Scotland (Chapman, 1975). However, Watson (1971) suggested that early casting may be associated with nutritional abundance during a snow-free season.

It also was suggested that antlers may function as a thermoregulatory organ during hot weather (Stonehouse, 1968), but Wika et al. (1975) demonstrated by thermography in reindeer that growing antlers

play a very minor role in regulating total body heat supply. Thus the effect of temperature on antler dynamics may be insignificant.

Antler dynamics may be more related to behavior and nutrition. French _et al_. (1956) demonstrated that when high levels of protein, energy, calcium and phosphorus were offered to white-tailed deer they produced larger, heavier antlers, with more numerous points compared to de deer offered rations deficient in these same nutrients.

The objective of the present investigation was to record antler growth and reproductive behavior of captive wapiti as indices of the circannual synchrony of day length and the internal biological oscillation.

5.0.0. METHODS AND MATERIALS

Records of behavior and antler development were made throughout the study on eight male wapiti. Photographs of each animal behind a grid with 12 x 6 inch (30.5 x 15.2 cm) squares were made each month between March and June, 1977 (Appendix 3).

5.1.0. RESULTS AND DISCUSSION

Pedicles were first apparent by palpation, in the first 2 weeks of September, 1976. Increased aggressiveness toward other wapiti and research attendants was observed during this same period. Shying away from fences and objects became quite noticeable. Previous to

this time the wapiti showed few signs of awareness of these same objects. The more dominant animals were observed mounting their pen mates when together as a group. The testes, although small, had descended in some of the males. Wislocki et al. (1947) demonstrated that when testosterone was administered to ovariectomized female white-tailed deer, pedicles could be grown. This suggested that testosterone was a prerequisite to pedicle formation. This was later confirmed by Goss et al. (1964). Thus, increased testosterone production occurred in the wapiti this may explain the increased aggressiveness and sexual activity observed when the pedicles were first appearing.

Antler growth began between January 16 and February 19, 1977, when the wapiti were approximately 8 months old (Table 6). Temperature appeared to have no relation to the initiation of antler growth,, although growth was first observed in two IN wapiti (Table 8). The animals that began antler growth first were also those animals that were heavier (Table 8) and had fewer problems with pre-weaning nutrition. Another factor contributing to the early appearance of antlers in the two IN wapiti may have been the reduced light intensity of the IN wapiti compared to the OUT wapiti, in accordance with Aschoff's rule (Quay, 1968).

Antlers grew rapidly and with unpredictable irregularity (Appendix 3C, Plates 2 & 3). Many of the animals later grew produced brow tines (1134 and 1136) and others branched tines (1128 and 1134). Glover (1953) also reported that a captive zoo wapiti produced a brow tine in the first year.

Wapiti 1138 had shorter antlers (Appendix 3C, Plate 4) than the other wapiti, probably as a result of being more easily excited.

Table 8. Initiation of antler development by wapiti calves.

Wapiti ID	Temperature Treatment	Date Antlers began growing	Body Weights Feb. 4/77(kg)
1137	IN	Jan. 16-22	154
1133	IN	16-22	142
1138	OUT	23-29	144
1136	OUT	23-29	141
1139	IN	Feb. 6-12	124
1135	IN	6-12	117
1134	OUT	13-19	144
1128	OUT	April 3	130

Wapiti 1138 was also difficult to handle. Wapiti 1133 and 1138 produced several protuberances along the shafts of the antler (Appendix 3A, Plate 3). These protuberances appeared to arise as a result of bumping them on the sides of the pens.

The antlers of wapiti 1136 and 1138 began to harden by the end of May. Some scraping of the velvet occurred in early June. The antler velvet of wapiti 1137 began to dry up at the beginning of April and subsequently was scraped off. This animal also showed some signs of rutting, but failed to show any signs of overt aggressiveness. On April 21, the antlers were removed 3 to 4 cm above the coronet of wapiti 1137. Some blood was still evident in the left antler stumps. The weight of the left and right antlers were 529 and 316 g, respectively. About mid-May new antlers began growing (Appendix 3A, Plate 1), and eventually enclosing the previous antler stumps by mid-July (Appendix 3A, Plate 2).

Growth of new antlers when the antlers of the previous year were still not shed were studied by Topinski (1975). Topinski (1975) demonstrated that by disturbing the hierarchy of a herd of white fallow deer (Dama dama) the resulting stress caused unilateral inhibition of antler casting and the growth of a new set of antlers in the dominant male. He suggested that corticosteroids may also have an important role in causing these antler anomalies.

CHAPTER 6

EFFECT OF SEASON AND TEMPERATURE ON HEMATOLOGY

Urea-N, hormones, alkaline phosphatase, and mineral constituents in the blood may be useful indicators of metabolic activity, disease and nutritional status of an animal. Several studies have been made on the chemical components of wapiti blood (Herin, 1968; Knight, 1969; Weber and Bliss, 1972; Pedersen and Pedersen, 1975), but very little has been reported on the effect of season and temperature on these parameters. Generally, animals which have been studied have been captured and immobilized with drugs or by mechanical means, thus increasing the possibility of hemoconcentration (Gartner, et al., 1969; Seal, et al., 1972a; Hyvarinen et al., 1976).

Knight (1969) measured serum concentrations of magnesium, phosphorous and calcium in December, January and February. He found serum magnesium declined, but calcium and phosphorous to suddenly rise in February. Weber and Bliss (1972) determined several blood constitutents of captive zoo animals and compared them to free-ranging wapiti. They found serum alkaline phosphatase to be greater in captive zoo wapiti than in wild wapiti. However, the captive wapiti were still growing (between 9 and 12 mo. of age), which may explain this difference. Serum concentrations of blood urea nitrogen (urea-N) were significantly greater in the free-ranging wapiti than in the zoo wapiti. Similar blood differences in zoo wapiti and free ranging wapiti were reported by Vaughn et al. (1973).

Bubenik et al. (1975) have shown that increased serum alkaline phosphatase levels occur in male white-tailed deer during the antler growing stage while low levels occur during antler inactivity. Alkaline phosphatase mobilizes phosphate for bone development and bone growth (Harper, 1973).

The effects of cold temperatures on thyroid hormones in various ruminants has been reviewed by Westra (1975) and investigated in sheep by Westra and Christopherson (1976) and Falconer (1976), but no information is available on this subject for wapiti. This is also true for the effect of season on thyroid activity, although some investigations have been reported for deer (Hoffman and Robinson, 1966; Seal et al., 1972b) and for reindeer (Yousef and Luick, 1977).

The objectives of this study were to clarify the effect of season and temperature on several blood parameters in growing wapiti offered a constant quality ration.

6.0.0. METHODS AND MATERIALS

Blood samples were drawn from all wapiti by jugular venipuncture into 10 to 15 ml vacutainers between 1200 and 1400 h at the beginning of every experiment. Packed cell volume (PCV), white blood cell count (WBC) and hemoglobin concentrations were made soon after the blood was obtained from the wapiti. Plasma (heparinized) and serum samples were frozen (-15 C) and stored for later analysis.

The PCV was determined by the microhematocrit method. White blood cell counts were made using the Unipet System (test 5805, Beaton and

Dickinson Co., N.J.) and the white blood cells were counted using a hemocytometer and microscope. Hemoglobin concentrations were determined using a hemoglobinometer (American Optical Corp., Scientific Instrument Div., Buffalo, N.Y.). Slides for counting differential white cells were prepared and stained in Wright's blood stain; 100 leukocytes were counted using the battlement procedure (Schalm et al., 1975).

Alkaline phosphatase determinations were made using the Phosphatrate Alkaline kit system (General Diagnostics Div., Warner-Lambert Co.) and measured in International units per liter (U/l) (One International unit is defined as the amount of enzyme that will liberate one μM of end product in one minute under conditions specified in the test). Standards were made as described by Babson et al. (1966).

Serum thyroxine (T_4) was determined from thawed serum samples using a Tetralute ^{125}I Reagent kit (Ames Company, Division Miles Laboratory, Inc., Elkhart, In. 46514) which uses a method described by Braverman et al. (1971). Serum 3,5,3'-triiodothyronine (T_3) concentrations were determined using a RIA-MAT circulating T_3 ^{125}I kit (Mallinckrodt Chemicals Works, St. Louis, Mo. 63147), a procedure based on the methods of Larson (1972), Lieblick and Utiger (1972) and Surks et al. (1972). The ^{125}I radioactivity was counted with a scintillation detector (Model No. OS 202 (V), Nuclear-Chicago, Corp) fitted with a 2 inch well-type thallium activiated sodium iodide crystal (Model No. XT2W0, Nuclear-Chicago Corp.) and monitored by a scaler (Model No. 8725, Nuclear-Chicago Corp.) adjusted with both windows open and set at a voltage of 875 volts.

Plasma concentrations of calcium (Ca), inorganic phosphate (P), creatinine and urea-N and serum protein concentrations were determined

by using ta Technicon Auto Analyzer system. Plasma calcium was determined by the method described by Kessler and Wolfman (1964); plasma P was determined by the method described by Fiske and Subbarow (1925); creatinine was determined by the saturated picric acid reaction method (Chasson et al., 1961); and plasma urea-N determined by the diacetyl monoxine reaction method described by Skeggs (1957) and Marsh et al. (1957). Serum protein was determined by a modified biuret reaction method described by Failing et al. (1960).

6.1.0. RESULTS AND DISCUSSION

Blood chemistry profiles obtained during the five experiments are shown in Tables 9 and 10. Also shown are values which were not included in the statistical analysis, taken in the summer and early fall of 1976. Seasonal effects were significant for all measured parameters except for serum protein. Temperature had no significant effect on any of the blood parameters except alkaline phosphatase.

6.1.1. PACKED CELL VOLUME AND HEMOGLOBIN

Season significantly affected ($P<0.001$) PCV and hemoglobin concentrations (Table 9). Packed cell volume increased from 28.5% in July, to 47.1% in June of the following year; and hemoglobin concentration increased from 10.4 to 16.2 g % in the same period. The adjusted mean for the period October to June for PCV and hemoglobin was respectively 41.4% and 16 g% Kitts et al. (1956) and Youatt et al. (1965) indicated

Table 9. Seasonal hematology of growing wapiti maintained on a high quality pelleted ration.

Time	PCV %	Hemo-globin g%	Total WBC /mm^3	Lympho-cytes %	Neutro-phils %	Eosino-phils %	Mono-cytes %	Baso-phils %
July 6/76	28.5 (1.0)*	10.4 (0.41)	6945 (428)	37.0 (3.5)	58.0 (3.4)	<1	2.0	1.4
Aug. 30/76	35.0 (0.89)	13.9 (0.50)	5175 (534)	-	-	-	-	-
Sept. 27/76	26.1 (1.4)	14.0 (0.47)	5364 (210)	56.2 (5.7)	37.3 (5.6)	3.32	2.4	<1
1976-1977								
October	39.7^{ab} (1.5)	15.6^{ab} (0.37)	4800^{a} (314)	44.0^{ab} (3.7)	50.2^{a} (3.6)	4.7	<1	1.8
December	40.2^{ab} (1.5)	16.2^{b} (0.37)	7950^{c} (314)	45.6^{ab} (3.7)	42.2^{a} (3.6)	8.14	1.6	1.6
February	35.1^{a} (1.5)	14.3^{a} (0.37)	5900^{ab} (314)	40.2^{a} (3.7)	48.5^{a} (3.6)	5.65	4.1	2.2
April	44.6^{bc} (1.9)	16.8^{b} (0.48)	7108^{bc} (405)	68.1^{c} (4.8)	26.5^{b} (4.7)	13.3	1.9	0
June	47.1^{c} (1.9)	16.2^{b} (0.48)	4958^{a} (405)	57.8^{bc} (4.8)	20.1^{b} (4.7)	13.8	2.2	1.1

abc - when subscripts differ between experiments (1,2 ... 5) the values are significantly different ($P<0.01$). Duncan's New Multiple Range Test.

*numbers in parenthesis are standard errors of the mean.

Table 10. Seasonal changes in plasma chemistry of growing wapiti maintained on a high quality pelleted ration.

Time	Serum Protein g%	Plasma Urea-N mg%	Plasma creatinine mg%	Plasma calcium mg%	Plasma Inorganic phosphate mg%
July 6/76	6.7	31.4	1.6	-	-
	(0.07)*	(1.4)	(0.04)	-	-
Aug. 30/76	-	26.2	1.5	-	-
		(2.0)	(0.05)		
Sept. 27/76	6.0	35.9	1.1	12.2	10.3
	(0.08)	(1.9)	(0.04)	(0.21)	(0.50)
1976-1977					
October	6.4	20.2^{a}	1.11^{a}	14.7^{a}	11.5^{a}
	(0.13)	(0.93)	(0.04)	(0.42)	(0.40)
December	6.0	25.2^{b}	1.34^{b}	12.5^{b}	11.2^{ab}
	(0.13)	(0.93)	(0.04)	(0.42)	(0.40)
February	6.3	24.9^{b}	1.41^{b}	12.2^{b}	10.0^{ab}
	(0.13)	(0.93)	(0.04)	(0.42)	(0.40)
April	6.5	21.7^{ab}	1.48^{b}	12.1^{b}	10.1^{ab}
	(0.16)	(1.2)	(0.05)	(0.55)	(0.52)
June	6.5	25.7^{b}	1.71^{c}	11.8^{b}	9.5^{b}
	(0.16)	(1.2)	(0.05)	(0.55)	(0.52)

abc - when subscripts differ between experiments (1,2...5) the values are significantly different from zero ($P<0.01$). Duncan's New Multiple Range Test.

*numbers in parenthesis are standard errors of the mean.

that the hematocrit and hemoglobin concentration were lower in fawns than in adult deer. The PCV and hemoglobin values obtained from the wapiti of the present study, were lower by 13 to 41% and 16 to 26%, respectively, than those reported by Herin (1968) and by Pedersen and Pedersen (1975), or those found in white-tailed deer (Ullrey et al., 1967), or in mule deer (Kitts et al., 1956; Rohwer et al., 1970). During the coldest month (December), PCV tended to be higher, but not significantly, in the OUT wapiti than in the IN wapiti. The PCV and hemoglobin concentrations in February were lower ($P<0.01$) than in the months that followed (April and June). Similar observations were made in cattle (Olsen, 1973).

6.1.2. WHITE BLOOD CELLS AND DIFFERENTIAL BLOOD CELL COUNTS

White blood cell count (WBC) displayed a cyclic pattern (Table 9). WBC were lower ($P<0.01$) in December and April than in any other month, while the WBC in July, August and September were similar to each other. The overall mean WBC was $6143/mm^3$. Pedersen and Pedersen (1975) reported WBC in adult wapiti of $8628/mm^3$ and Herin (1968) reported WBC of $5559/mm^3$.

The overall mean of the lymphocytes and neutrophils was 51.1 and 37.5%, respectively. Pedersen and Pedersen (1975) reported a mean lymphocyte distribution of 25%, and a mean neutrophil distribution of 68%. Vaughn et al. (1973) reported lymphocyte values of 28% and 36% for females and males, respectively, and neutrophil values of 39% and 28% for females and males, respectively. According to Schalm et al. (1975) stress may cause eosinophils to decrease and lymphocytes to increase.

Lee et al. (1976) reported that when the ambient temperature rose, dairy cattee exhibited leukocytosis, largely as a result of an increased number of circulating neutrophils, as compared to lymphocytes. The average eosinophils, monocytes and basophils counted in this study, were within the range reported in other deer species (Drescher-Kaden and Hoppes, 1973).

6.1.3. SERUM PROTEIN

Season had no effect on serum protein concentrations in this study (Table 10, Appendix 5). The overall mean serum protein concentration of the wapiti (Table 10) was 6.3 g%, similar to that reported by Weber and Bliss (1973), and within the range reported by Herin (1968) and Pedersen and Pedersen (1975). The overall mean values reported by Pedersen and Pedersen (1975) for yearling males and females were, respectively, 6.81 and 6.66 g%. Weber and Bliss (1972) reported protein concentrations of 6.0 g% for yearlings, and 6.1 g% for nine-month-old wapiti calves. Animals fed high protein rations often have higher serum protein concentrations than animals fed low protein rations and may reflect the protein reserve status during times of high protein intake (Ullrey et al., 1967).

6.1.4. PLASMA UREA-N

Plasma urea-N (PUN) was significantly affected by season ($P<0.01$) and was lower ($P<0.01$) in October than in December, February and June (Table 10).

Table 11. Serum concentrations of calcium (Ca), magnesium (Mg), phosphorous (P), sodium (Na) and potassium (K) in samples obtained May 15, 1977.*

	Plasma serum concentrations				
ELK ID	Ca mg%	Mg mg%	P[2] mg%	Na mEq/1	K mEq/1
1128	8.6	1.98	10.8	154.3	5.77
1129	8.8	1.94	9.8	153.5	6.00
1131	9.6	2.06	9.5	160.0	5.67
1132	8.3	1.87	9.8	155.6	5.36
1133	9.6	2.30	10.8	155.2	5.90
1134	8.4	2.14	10.1	160.0	5.67
1136	8.3	1.90	12.2	160.4	5.56
1137	8.2	1.84	12.2	155.7	5.54
1138	8.2	1.98	13.4	157.8	5.20
Mean	8.7	2.00	11.0	156.9	5.63

*Analysis done by the Veterinary Services Division, O.S. Longman Building, 6909 - 116 St., Edmonton, Alberta. T6H 4P2.

P was analysed by the method described by Fiske and Subbarow (1925), and the other serum elements were determined by atomic absorption spectrometry.

The reported mean for PUN for the entire year was 23.6 mg%. Weber and Bliss (1973) reported blood urea-N values of 16.5 to 20.0 mg% for calf and yearling wapiti, and Pedersen and Pedersen (1975) reported serum urea-N values of 25.0 to 27.5 mg% for male and female yearlings. The PUN values of the present study were well within the range reported for deer and bovine species summarized by Barrett and Chalmers (1977).

PUN was related ($P<0.01$) to urea-N recycled to the digestive tract ($r=0.4418$), which will be discussed in the final section of this thesis. PUN may be used as a parameter for predicting the nutritional status of ruminants, however, as Preston _et al_. (1965) have indicated, this relationship can be modified by other factors (Kirk and Walker, 1976a, 1976b).

6.1.5. PLASMA CREATININE

Plasma cratinine (PC) levels changed seasonally (P 0.01)(Table 10). PC was 1.6 mg% in July, decreased to 1.1 mg% in September and October, and gradually increased to 1.7 mg% in June of the following year.

The values obtained in the present study, were similar to those reported by Weber and Bliss (1975) in young and adult wapiti (range 0.9 to 1.8 mg%; $\bar{x}$ = 1.5 mg%), as well as to those reported in mule deer and black-tailed deer (Dhindsa _et al_., 1975). High PC levels are indicative of renal damage and can arise from physical stress of capturing (Harthoorn, 1973).

6.1.6. PLASMA INORGANIC PHOSPHATE AND SERUM ALKALINE PHOSPHATASE

Season had a significant effect ($P<0.01$) on plasma inorganic phosphorus (Table 10). It decreased from a high in October to a low in June of the following year. In September, plasma P was low, similar to the values obtained in April. There was a significant ($P<0.05$) temperature and unit interaction indicating that the plasma P of the IN wapiti of unit 2 (9.8 mg%) were significantly lower than that of the OUT wapiti of unit 2 (11.3 mg%).

Serum levels of P were determined in May (Table 11). No differences were observed between plasma and serum P concentrations, similar to that reported by Telani _et al_. (1976), in cattle.

Sex differences in serum P were quite apparent (Table 11). The average serum P level was 9.7 mg% for the females (wapiti 1129, 1131, 1132) compared to 11.6 mg% for the males. Pedersen and Pedersen (1975) reported similar serum P differences between yearling males (6.57 mg%) and females (6.01 mg%), as well as, lower concentrations. Lower concentrations of serum P in adults (4.70 mg%) than in yearlings were also found. Values of 8 to 10.3 mg% have been reported in red deer (Drescher-Kaden, 1974), values of 3.7 to 6.5 mg% have been reported in sheep fed low and high amounts of P, respectively (McDonald and Belonje, 1975), and values of 7.6 to 11.4 mg% serum P have been reported in white-tailed deer fed 0.22 to 0.62% Ca, respectively (Ullrey _et al_., 1973). Young growing animals have higher plasma P levels than adults and this is usually related to bone growth (Maynard and Loosli, 1969), which may account for the higher concentrations of P in the wapiti of this study, compared to that found in other cervids (Ullrey _et al_., 1975).

Serum alkaline phosphatase is a diagnostic test for determining inadequate P intake, bone abnormalities and liver disease. Alkaline phosphatase hydrolyzes organic phosphate esters and is directly related to oesteoblast activity (Maynard and Loosli, 1969).

Higher levels ($P<0.01$) of serum alkaline phosphatase concentrations were found in April and June than that found in December and February (Figure 4). Temperature exposure also had a significant effect; the IN wapiti had higher ($P<0.01$) serum levels of alkaline phosphatase than the OUT wapiti. In addition, the IN wapiti had a greater ($P<0.01$) serum alkaline phosphatase concentrations than the OUT wapiti in February, April and June (Figure 4).

There was also a significant unit and temperature interaction (Table 1, Appendix 5). The serum alkaline phosphatase levels for the IN and OUT wapiti of unit 1 were, respectively, 125.2 and 73.6 U/1, and for the IN and OUT wapiti of unit 2 were, respectively, 166.2 and 117.4 U/1. No differences ($P<0.01$) were obtained between the IN and OUT wapiti of unit 1 and 2. This interaction, together with the experiment (season) and temperature interaction, suggested that wapiti 1133 and 1137 (IN wapiti of unit 2) may have entered the summer growth and antler development phase sooner and more rapidly than the OUT wapiti. This further suggested that photoperiod differences may have occurred between the two temperature treatments.

Serum alkaline phosphatase levels were nearly twice as high as those reported in mature wapiti by Weber and Bliss (1972), slightly lower than in male yearlings as reported by Pedersen and Pedersen (1975), and similar to the levels reported by Vaughn et al. (1973). Bjarghov et al. (1976) observed that reindeer fed a high protein-energy ration

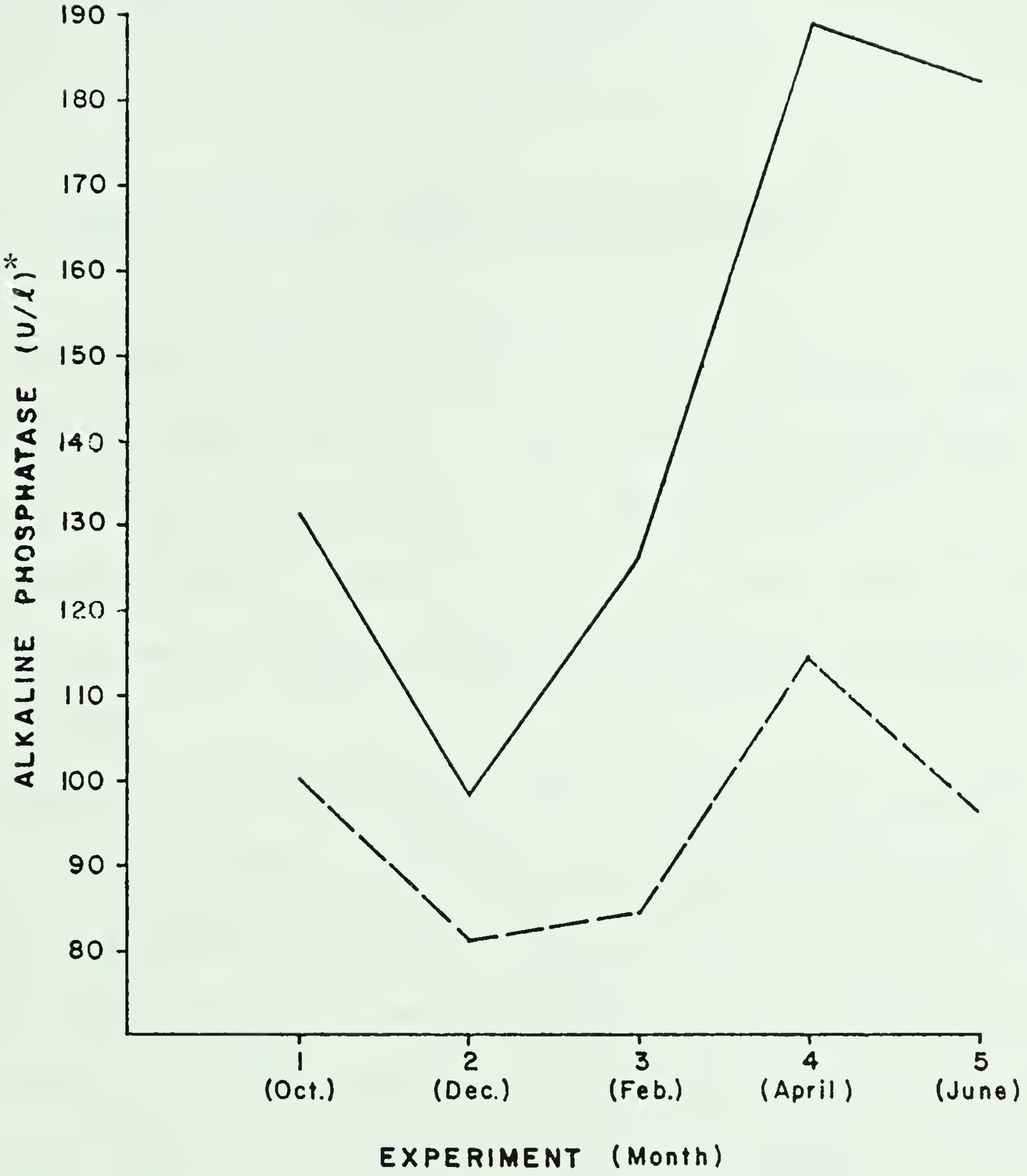

Figure 4. The effect of temperature and season on serum alkaline phosphatase.
(IN wapiti, ———; OUT wapiti, - - - -)
*U/ℓ = international units per liter.

had serum alkaline phosphatase levels of 300 U/l in December and 500 U/l in April, nearly twice the concentrations determined in wapiti. Bubenik et al. (1975) demonstrated that during the antler growing phase in white-tailed deer, plasma alkaline phosphatase levels were similar to the levels determined in this study.

6.1.7. PLASMA CALCIUM AND OTHER BLOOD ELECTROLYTES

Season had a significant effect ($P<0.01$) on plasma Ca (Table 10). Plasma Ca was higher ($P<0.01$) in October than in any other month. In white-tailed deer, N and energy intake, season (Seal et al., 1972b) and levels of Ca and P intake (Ullrey et al., 1973, 1975), all had no effect on plasma Ca. Similar findings were reported in reindeer (Bjarghov et al., 1976).

Plasma Ca levels were similar to those reported in red deer and roe deer (Drescher-Kaden, 1974), and in domestic sheep receiving high dietary Ca (McDonald and Belonje, 1975). The serum Ca levels (Table 11) were lower by 0.5 to 1 mg%, compared to those of Pedersen and Pedersen (1975) and Herin (1968). Serum Ca in white-tailed deer (Ullrey et al., 1973, 1975) were 3 to 4 mg% higher than those obtained in the wapiti of this study.

Plasma Ca (Table 10) was higher than the serum Ca concentrations (Table 11); this was expected since Ca is an element necessary for clotting and will be taken up into the blood clot.

The average serum Mg, Na and K concentrations were 2.00 mg%, 156.9 mEq/l and mEq/l, respectively (Table 11). The serum Mg levels

were higher than those reported for reindeer (1.00 to 1.20 mg%)(Bjarghov et al., 1976), and similar to those reported in white-tailed deer (Ullrey et al., 1973, 1975), pronghorns (Antilocapra americana)(Barrett and Chalmers, 1977), red deer and roe deer (Drescher-Kaden, 1974). Serum Na was higher in wapiti of this study, than reported by Herin (1963), but similar to those reported in pronghorns (Barrett and Chalmers, 1977), reindeer (Bjarghov *et al.*, 1976; Hyvarinen *et al.*, 1977) and moose (Alces alces) (Le Resche *et al.*, 1974). Serum K levels in wapiti during May were similar to those reported in other cervids.

6.1.8. THYROID HORMONES

Serum T_4 and T_3 concentrations were significantly affected ($P<0.01$) by season (Figure 5). Thyroxine and T_3 serum concentrations decreased from a maximum level of 9.0 µg% and 161 ng% respectively in July to 4.1 µg% and 57.1 ng% respectively in June of the following year. Both serum levels of T_4 and T_3 fell rapidly in August and September, but then rose again in October ($P<0.01$), and fell thereafter, to lower levels as shown in Figure 5. Serum T_3 levels in October were significantly higher ($P<0.01$) than that in December. In December the T_3 values were significantly higher ($P<0.01$) than those obtained in February, April and June. The serum T_4 levels in December, February and April were not significantly different from each other ($P>0.01$) but the October T_4 levels were significantly higher ($P<0.01$) than those in April and June, and the T_4 levels in June were significantly lower ($P<0.01$) than those in October, December and February.

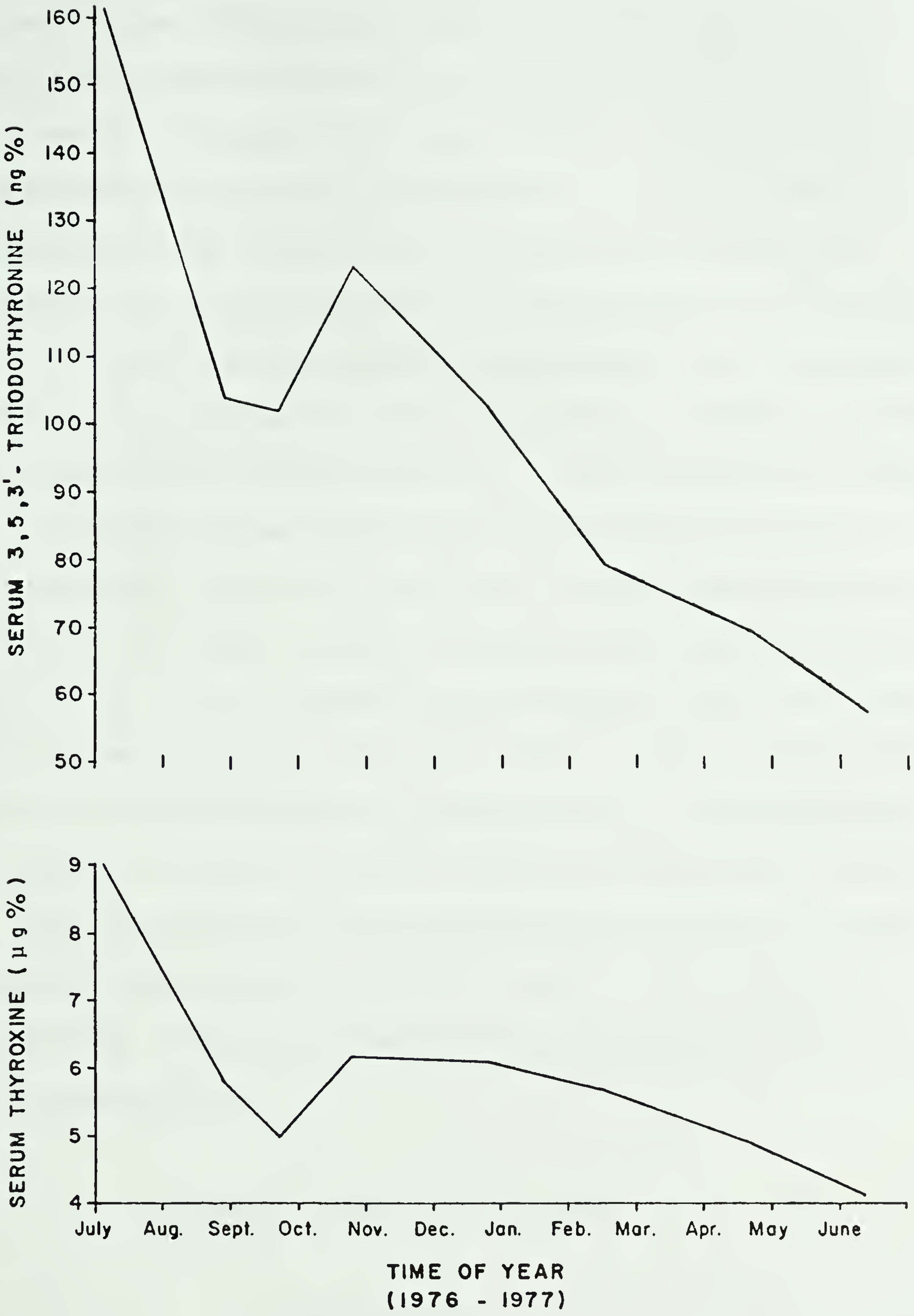

Figure 5. The effect of season on serum thyroxine and serum 3,5,3'-triiodothyronine.

Season had no effect on serum T_4 in white-tailed deer fed a supplemented diet of white cedar (high diet), whereas serum T_4 was significantly reduced ($P<0.01$) in deer fed only white cedar during March compared to December (Seal et al., 1972 b). Yousef and Luick (1971) found no effect of season on T_4 turnover rate, T_4 secretion rate and plasma protein bound iodine levels in reindeer and concluded that temperature had little or no effect on thyroid activity. They suggested that the insulative properties of winter pelage and other physiological and behavioral mechanisms in reindeer decreased the need for an increased metabolic rate. More work is required to clarify the effects of season, age and the level of feed intake on the thyroid of wild ruminants.

The overall means for T_4 and T_3 were 5.4 μg% and 86.1 ng% respectively. The overall T_4 mean was similar to that found in cattle (Miller et al., 1974), in bovine calves (Curtis and Abrams, 1977), and in moose (LeResche et al., 1974). The overall T_4 mean concentration in wapiti was one-half the mean concentration found in white-tailed deer (Seal et al., 1972 b), and in sheep (Westra and Christopherson, 1976).

Serum T_4 concentrations were significantly ($P<0.0001$) correlated to serum T_3 concentrations ($r=0.5925$), similar to that reported by Larson (1972). The following relationship was calculated when T_4 was regressed on T_3:

$$T_3(\text{ng\%}) = -109.4 + 36.9\ T_4(\mu\text{g\%}) \qquad (3)$$

$$\text{S.E.} = 0.0063$$

In their review, Bernal and Refetoff (1977) reported that elevated

serum T_4 and T_3 levels are associated directly with an increased protein synthesis, and increased synthesis, mobilization and degradation of lipids, and a modified carbohydrate metabolism. These effects resulted in an increased calorgenic activity. Yeh and Moog (1977) demonstrated in rats that thyroid hormones are also necessary, besides glucocorticoids, for intestinal epithelial maturation, and intestinal enzyme formation during the weaning period. Mosekilde et al. (1977) demonstrated that elevated levels of thyroid hormones in man stimulate osteoclastic bone resorption in both trabecular bone and cortical bone. Thus, it is during the early growing period that thyroid hormones are important for growth and differentiation of new cells. This may help to explain the high serum T_4 and T_3 levels during the summer and autumn months in the wapiti. Lower levels of T_3 concentrations were observed in wapiti 1138 and 1139 (85 and 94 ng%, respectively) in the July-August period. Wapiti 1139 also showed a slower growth rate during this same period. Lower thyroid activity has been suggested to be related to a depressed DNA activity, lower body weight gain and decreased skeletal growth in muskrats (Ondatra zibethica) during the winter (Alesiuk and Frohlinger, 1971). The high serum T_4 and T_3 levels during the summer may also be associated with age, since it has been suggested that fewer receptor sites may be available in very young animals (De Groot et al., 1977).

CHAPTER 7

EFFECT OF SEASON AND TEMPERATURE ON DIGESTION

Digestibility of forages consumed by free-ranging wapiti changes throughout the year (Nelson and Leege, 1978) and is often interpreted as a plant attribute (Ward, 1971). However there are several animal factors which also may contribute to seasonal changes in the efficiency of forage utilization. Deer show a marked decline in food intake sometime after November (French et al., 1955; Ozoga and Verme, 1970; Short, 1975) and increase food intake to high levels again in spring and summer. Recently, Holter et al. (1977) reported similar observations in white-tailed deer. They also found apparent digestibilities (hereafter called digestibility) of DM, organic nutrients and energy (E) variable throughout the year. Animal variation was significant for most variables measured. Throughout their study protein concentrations in the feed were progressively reduced from 22% at weaning to 11% 15 months later. Therefore this change in protein content may have had confounding effects upon the other nutritive components and animal growth characteristics. Kirkpatrick et al. (1975) found increased levels of protein to directly affect weight gain in 3.5 month-old white-tailed deer.

Moen (1973 and 1976) and Ozoga and Gysel (1972) suggested that it may be more advantageous for deer to reduce feed intake and thereby reduce foraging, especially during periods of low temperatures when conserving energy as stored fat would be more important. Holter et al. (1975) found energy expenditures in deer to be less in winter than in any of the other seasons and suggested that the increased pelage insulation

and time spent lying down during the winter may have helped to maintain low energy expenditure. Thus, low food consumption by cervids during cold winter days may approach a more optimum energy budget by reducing activity and exposure to cold (Moen, 1976).

Cold temperatures have been shown to decrease the digestibilities of DM, energy (E) and acid detergent fiber (ADF) in sheep (Westra and Christopherson, 1976) and the digestibility of DM in cattle and sheep (Christopherson, 1976). The decrease in digestibility of DM in sheep exposed to cold compared to sheep exposed to warm temperatures was shown by Kennedy et al. (1976) to occur as a result of an increased rate of passage of digesta from the rumen with a consequent reduced rate of fermentation in the rumen. Westra and Christopherson (1976) observed an increase in reticulum motility in cold exposed sheep (1.3 C) compared to sheep exposed to warm temperatures (21.2 C). Nitrogen digestibility remained relatively stable in sheep exposed to both temperature treatments and it was suggested by Kennedy et al. (1976) that the cold exposed sheep may have had an increased turnover of urea-N as a result of the lower concentrations of rumen ammonia.

The conversion of protein and non-protein nitrogen to ammonia in the rumen of domestic ruminants has been observed to have a positive and direct relationship with cellulose digestion (el-Shazly et al., 1961; Little et al., 1963). Ammonia is a necessary nutrient for some ruminal bacteria (Bryant, 1961). Leibholz and Hartmann (1972) observed that low available nitrogen in the diets in sheep (1.4 g compared to 16.1 g nitrogen per day) significantly depressed the digestibility of organic matter. These observations have been confirmed by others

(Broster, 1973; Jones *et al.*, 1973; Johnson, 1976; Donnelly and Hutton, 1976). Inadequate nitrogen levels have been shown to reduce the rate of passage of digesta in sheep (Leibholz and Hartmann, 1972). In turn, a reduced rate of passage may reduce DM intake (Freer *et al.*, 1962; Campling, 1970). Considering all these effects of feed quality and feed quantity throughout a given year little information is available as to the effects of photoperiod *per se* on digestion.

The partitioned effects of temperature and season (which is understood in this thesis to include the covariates of photoperiod and age of the animal) on digestion have not been studied in wapiti. The present investigation was designed to determine the effects of temperature within seasons and the effect of season on digestion of feed by growing wapiti. In particular, the digestion parameters investigated were the digestibility of feed and the rate of passage of digesta.

7.0.0. METHODS AND MATERIALS

The experiments for determining digestibility and the turnover time of digesta, as well as the mean retention time (MRT) of digesta were done simultaneously with the ^{14}C-urea infusion a single dose of 6 to 8 μ Ci of ^{103}Ru (see Appendix 4) was administered. The ^{103}Ru complex was prepared as described by Tan *et al*. (1971). In the first two of five experiments, this marker (^{103}Ru) was administered orally by placing it on the back of the tongue with a 5 ml syringe. In the last three experiments, the ^{103}Ru was administered intraruminally into the mid-dorsal region of the rumen on the left side of the animal using

a 2 1/2" 17-gauge needle fitted with a 3-way valve and a 5 ml syringe. Each time this operation was performed, the ^{103}Ru dose was flushed out of the syringe with water before retracting the needle from the rumen. In experiment 4 of week 1, a 1 1/2" needle was substituted for a 2 1/2" needle. The animals showed few signs of discomfort or excitability as a result of these procedures. This latter method of administration was used because there was some doubt of whether the ^{103}Ru dose entered the rumen completely before passing into the post-ruminal digestive tract.

The first fecal sample was collected 10 h after the radioactive dose was administered. Subsequent fecal samples were collected every 3 h for the next 36 h and then at increasingly extended intervals of 6, 8, 12 and 24 hours until the trial was completed. Several feed samples were collected during each trial for later analysis.

The wet feces were mixed, weighed and at least 10% was saved. The fecal samples were air-dried at 65 C and ground in a food blender.

The macro-Kjeldahl method (Association of Official Agricultural Chemists - AOAC, 1975) was used for the determination of N in urine. Gross energy (E) was determined using a Parr bomb calorimeter (Model N 101A). Neutral detergent fiber (NDF) determinations were made as described by the AOAC (1975). Analysis of fecal and feed nitrogen ether extract (fat) and ADF were done by the Alberta Agriculture Soil and Feed Testing Laboratory, Edmonton, according to the procedures outlined in the AOAC (1975). Hemicellulose was calculated by difference between ADF and NDF. Apparent digestiblity coefficients for E, N, ether extract, ADF and NDF and percent N retention were calculated. Water intakes were measured to the nearest 10 ml, and urine output measured to the nearest milliliter. Fecal samples were weighed into Beckman

vials and counted for 10 to 20 minutes per sample by a Beckman Counting System (Beckman Instruments, Fullerton, Co.). Mean retention time was calculated as described by Faichney (1975):

$$MRT = \sum_{i=1}^{n} t_i M_i$$

where, t_i is the time elapsed between dosing and the mid-point of the i^{th} time interval and m_i is the fraction of the amount of the marker excreted in the i^{th} time interval.

Transit time and the rate constants in a two-compartment physical model, simulating passage of a marker through the digestive tract were estimated. Transit time (TT) is defined as time it takes a tracer to pass through the omasum, abomasum and intestinal tract. The rate constant is defined as the fraction of tracer lost from a defined compartment per unit time. The three variables were predicted by a least squares computer program (Dixon, 1973) to fit the following relationship described by Grovum and Phillips (1973):

$$R(\%) = 100 \left(\frac{k_2 - k_1 + k_1 e^{k_2(t-TT)} - k_2 e^{k_1(t-TT)}}{k_2 - k_1} \right)$$

where: R = accumulative recovery of ^{103}Ru in feces

k_1 = rate constant related to tracer kinetics of reticulorumen

k_2 = rate constant related to tracer kinetics of hind gut

The turnover time was calculated by the summation of the transit time and the reciprocals of the k_1 and k_2 values (Shipley and Clark, 1972).

The excretion pattern of ^{103}Ru of wapiti 1138 (OUT wapiti) and 1139 (IN wapiti) of experiment 1 did not fit the equation derived by Grovum and Phillips (1973) shown in Table 8, Appendix 4, because the k_1 and k_2 values were restricted to a maximum of 1 and the least squares program could not satisfy the desired epsilon value of 0.0005. For the analysis of variance, the k_2 and transit time values for wapiti 1138 and 1139 were estimated by calculating the mean value of the other wapiti in the same experiment. When the derived values of wapiti 1139 and 1135 were included in the analysis of variance the results were uninterpretable; therefore, they were not included.

7.1.0. RESULTS

7.1.1. NUTRIENT INTAKE

Season significantly affected ($P<0.01$) feed consumption of wapiti. The level of average daily DM intake (g/d) tended to be cyclic and increased only slightly in this time period (Figure 6). When average feed intake was calculated on a metabolic weight basis ($/w^{.75}$), it dropped markedly ($P<0.01$) after October in both temperature treatments and continued to drop until April. DM intake/$w^{.75}$ by the IN wapiti tended to increase in June compared to the February and April levels, but not significantly ($P>0.05$). During March, wapiti 1137 (IN wapiti)

increased its DM intake (g/d) markedly (Figure 6) and the increased DM intake (g/d) paralleled an increased rate of weight gain.

Digestible energy (DE) intakes were 1326, 1060, 1000, 893 and 1090 kJ/$w^{.75}$kg/d for October, December, February, April and June, respectively. DE intake was significantly higher ($P<0.01$) in October than in any other month. DE intake/$w^{.75}$ was negatively correlated ($P<0.01$) with body weight ($r = -0.474$).

Temperature influenced DM intake (Figure 7), but not significantly ($P>0.05$). DM intake tended to be lower in the IN wapiti than the OUT wapiti, except in June when DM intake of the IN wapiti was greater than the OUT wapiti. The female and IN wapiti (Figure 6) had similar average cyclic DM intakes as the OUT wapiti which suggested that factors other than temperature were important.

Weather changes appeared to influence behavior patterns which may have indirectly contributed to changes in feed intake. About 12 to 24 h before a storm, or a sudden fall in temperature, both IN and OUT wapiti displayed a nervous excitement and consumed very little feed. They also were easily aroused, cried when approached and paced back and forth in a stereotype manner. After the weather changed, the wapiti settled down and resumed normal activities. When temperature rose, the wapiti appeared to be more playful, and had a zest for running and jumping. They also had a more placid disposition and tended to lie down for longer periods. During periods of cold they had a more irritable disposition and appeared to walk more stiffly.

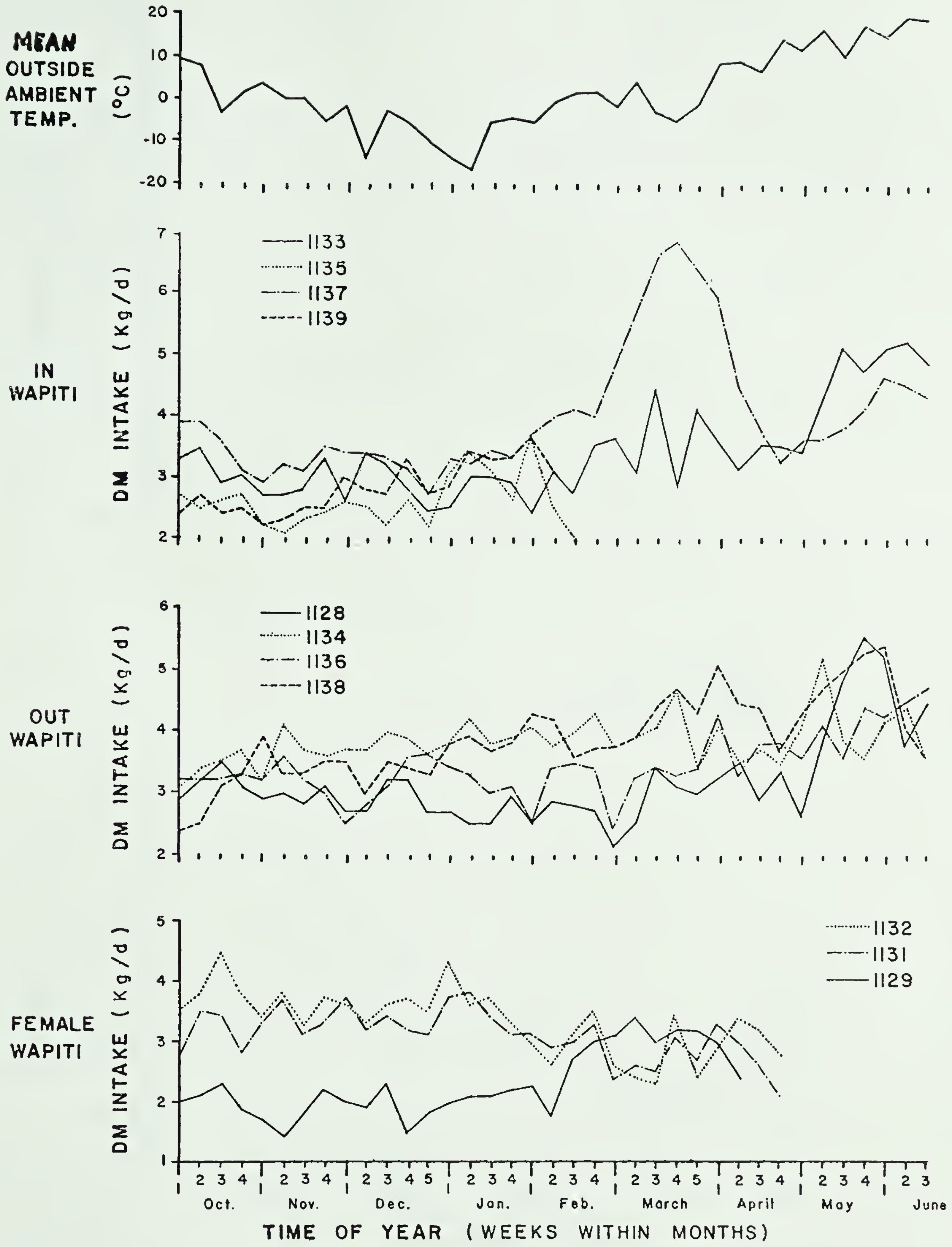

Figure 6. Average daily DM intakes (g/d) (7 d means) of male IN and OUT wapiti and female wapiti, and mean outside ambient temperature pattern (7 d means).

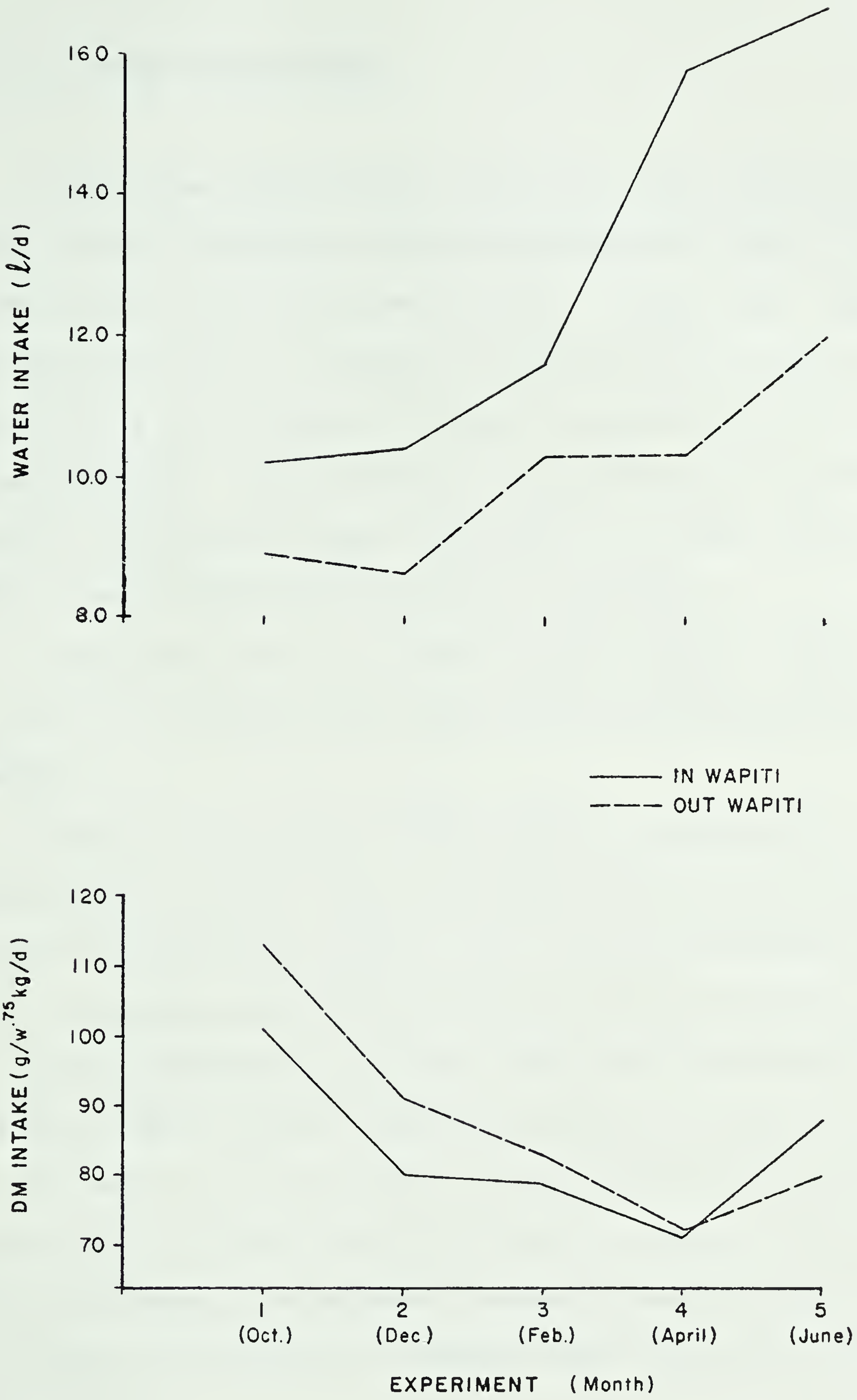

Figure 7. The effect of season and temperature on DM intake ($g/w^{.75}kg/d$) and water intake (l/d).

7.1.2. WATER AND SALT INTAKE

Water intake (ml/d) (Figure 7) and total water intake (ml/$w^{.82}$kg/d) which include the water in feed and drinking water (Table 12) were significantly ($P<0.01$) affected by season. Total daily water intake (ml/$w^{.82}$kg) was greater in October than in the other 4 months. Water intake (g/d) as shown in Figure 7 is biased by the increased growth with time. Macfarlane and Howard (1972) found that water intake based on the metabolic weight coefficient of $w^{.82}$ gave the best relationship of water intake with body weight in ruminants.

Temperature also affected water intake (Figure 7). Water intake (l/d) in the OUT wapiti was significantly lower ($P<0.01$) than in the IN wapiti.

When the mean total water intake/$w^{.82}$ was expressed as a ratio of the mean DM intake/$w^{.75}$ (water/DM) (Table 12), the values were relatively constant for the first 3 months, rose in April and decreased again in June. The higher water/DM intake during April may have been the result of higher temperatures than normal, however water intakes/$w^{.82}$ for the IN and OUT wapiti did not change during the last 3 months. In addition, if this were true, the OUT wapiti may have increased their water intake more than the IN wapiti, since the IN wapiti were in a controlled temperature environment. DM intake/$w^{.75}$ dropped slightly in April from that in February, and in June rose slightly higher than that in February (Figure 7).

Total daily water intake (ml/$w^{.82}$kg) was significantly ($P<0.01$) correlated with DM intake (g/$w^{.75}$kg/d) ($r=0.562$). When total daily water intake (ml/$w^{.82}$kg) (Wint) was regressed on DM intake (DMint) the

Table 12. Dry matter and water intake by growing wapiti offered a pelleted ration during the period of October, 1976. to June, 1977.

	MONTH				
Parameter	Oct.	Dec.	Feb.	Apr.	Jun.
DM intake (g/d)					
IN wapiti	2725	2707	3149	3975	5006
OUT wapiti	3266	3241	3419	3335	3937
Total water intake (g/$w^{.82}$kg/d)					
IN wapiti	273.2^{a} (16.1)**	221.4^{b} (16.1)	204.6^{b} (16.1)	201.8^{b} (24.6)	203.6^{b} (24.6)
OUT wapiti	225.8^{a} (16.1)	173.5^{b} (16.1)	177.8^{b} (16.1)	155.0^{b} (16.1)	168.5^{b} (16.1)
Water/DM intake*					
IN wapiti	2.69	2.78	2.59	2.83	2.32
OUT wapiti	2.00	1.90	2.15	2.16	2.12

ab – when subscripts differ within rows the mean values are significantly different from zero ($P<0.01$). Duncan's New Multiple Range Test.

* – Ratio of total water intake (ml/$w^{.82}$kg/d to DM intake (g/$w^{.75}$kg/d).

** – numbers in parentheses are standard errors of the mean.

following equation was derived:

$$\text{Wint } (\text{ml}/\text{w}^{.82}\text{kg}/\text{d}) = 53.82 + \text{DMint } (\text{g}/\text{w}^{.75}\text{kg}/\text{d}) \qquad (4)$$

$$\text{S.E.} = 0.42$$

Intake of DM (g/d) was also related ($P<0.01$) to water intake ml/d ($r=0.684$).

Cobalt-iodized salt was weighed September 20, and again November 19, 1976. The salt intake measured during this period was approximately 300 g for the IN wapiti and 180 g for the OUT wapiti. When salt consumed by the female wapiti was included with that consumed by the male wapiti the overall average intake was approximately 265 g. After November very little or no salt was consumed (weighed again in April, 1977).

7.1.3. APPARENT DIGESTIBILITY

Season and level of intake had a significant effect ($P<0.01$) on the digestibility of all fractions except NDF (Figure 8). The mean digestibility of DM in December and February increased approximately 2 percentage units from that in October. The mean digestibility of DM in April and June was significantly greater ($P<0.01$) than that in October. The digestibility of E ran parallel and slightly lower and the digestibility of N ran parallel and slightly higher than the digestibility of

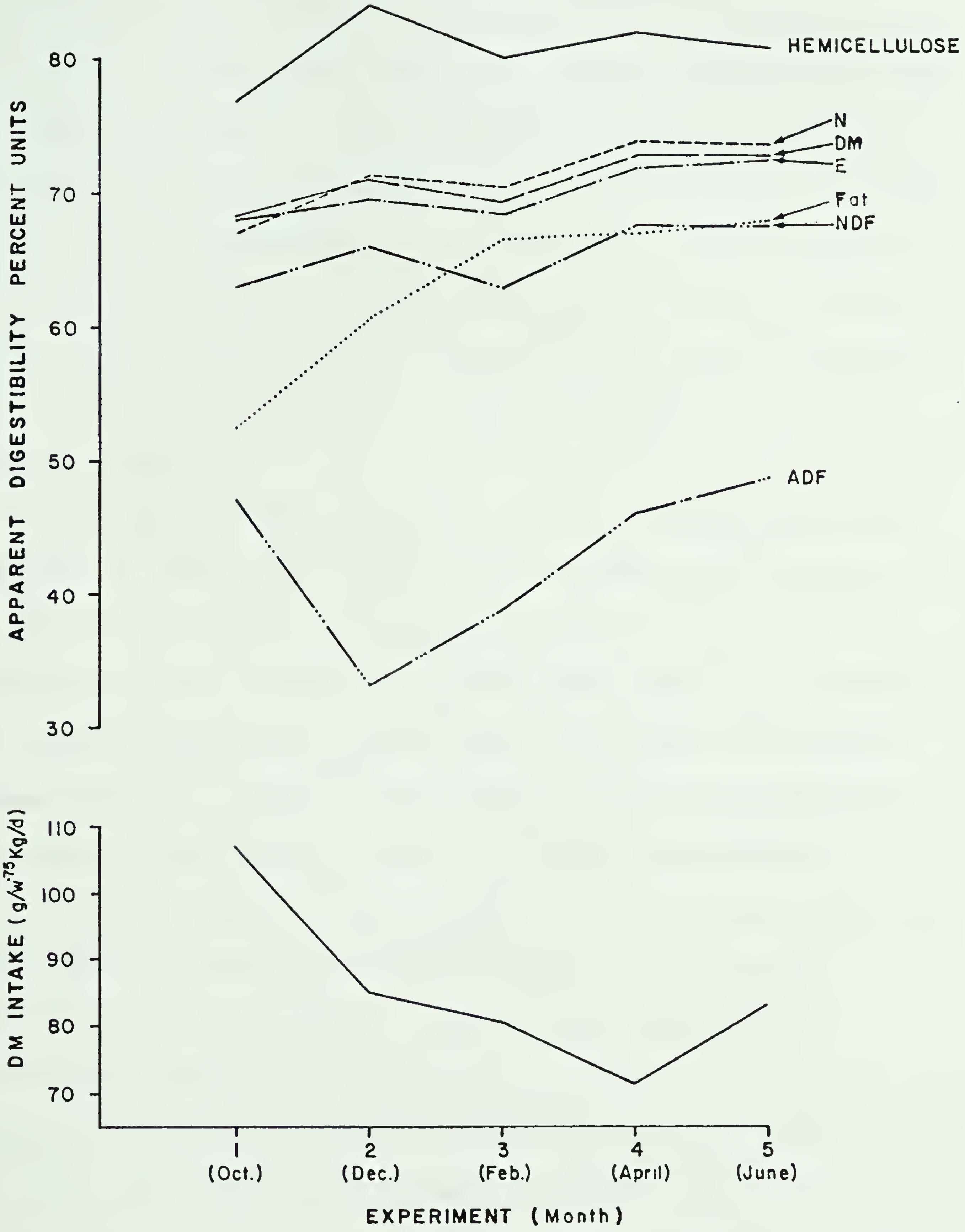

Figure 8. The effect of season on DM intake and on apparent digestibility of hemicellulose, N, DM, E, fat, NDF and ADF. (DM - dry matter; N - nitrogen; E - gross energy; fat - ether extract; NDF - neutral detergent fiber; ADF - acid detergent fiber).

DM across seasons. The digestibility of hemicellulose was significantly lower ($P<0.01$) in October than in December, whereas, in February, April and June the values were not significantly different ($P>0.05$) than those in October and December. The digestibility of fat was significantly lower ($P<0.01$) in October than in December, and in December the digestibility of fat was significantly lower ($P<0.01$) than in either February, April or June. The digestibility of ADF behaved in an opposite manner to that of hemicellulose and fat. Digestibilities of ADF were significantly ($P<0.01$) higher in October, April and June than they were in December and February.

Temperature also had a significant effect on digestion in wapiti. An example of this effect of temperature is illustrated in Figure 9 for the digestibility of N. The digestibility of E, N, ADF and NDF were significantly lower ($P<0.05$) in the OUT wapiti than in the IN wapiti. The outside temperatures during February were warmer than those in December (Figure 1), and the digestibility of the various nutritive components of the OUT wapiti tended to be equal to, or slightly greater than the values of the IN wapiti. Despite the fact that cold outside ambient temperatures reduced the digestibilities of E, N, NDF ($P<0.01$), and DM ($P<0.05$), and fat and hemicellulose ($P>0.05$) only slightly, the digestibility of these same components in both IN and OUT wapiti generally increased during the winter season from the levels obtained in October and December. Not only was there a depressed digestibility of ADF by season in December and February compared to October, April and June, but the cold outside temperatures in December further reduced ($P<0.01$) the digestibility of ADF in the OUT

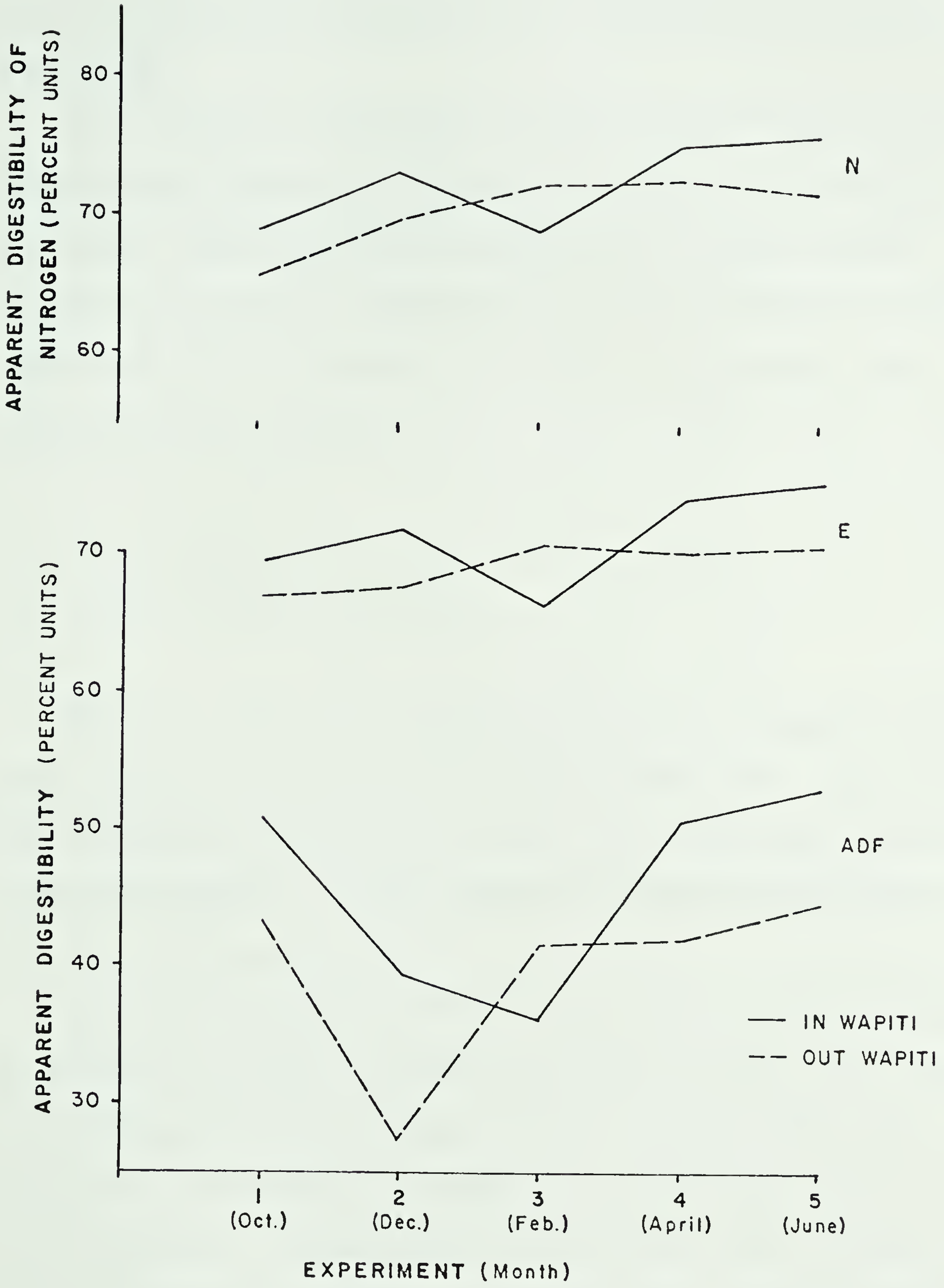

Figure 9. The effect of season and temperature on apparent digestibility of N, E and ADF.
(N - nitrogen; E - gross energy; ADF - acid detergent fiber).

wapiti compared to the IN wapiti (Figure 9). A significant ($P<0.025$) season and temperature interaction also occurred for the digestibilities of E and ADF.

The correlation coefficients of DM intake/$w^{.75}$ with E, N, fat, ADF and NDF digestibility were respectively -0.266, -0.439, -0.632, 0.108 and -0.161, with only N and fat significantly related ($P<0.01$). The digestibility of DM was significantly correlated ($P<0.01$) to the digestibilities of N ($r=0.856$), E ($r=0.871$), fat ($r=0.699$), ADF ($r=0.462$) and NDF ($r=0.811$).

7.1.4. RATE OF PASSAGE OF DIGESTA

The MRT of ^{103}Ru within the digestive tract was significantly lower ($P<0.01$) in October than in February (Table 13). Mean retention time in December and June did not differ from those values obtained in October and February. The MRT estimated for April was the mean of two OUT wapiti (1128 and 1138) only.

Season had a significant effect on the rate constants k_1 and k_2. The estimated k_1 value in December was greater ($P<0.05$) than in February, but no different than the values in October and June (Table 13). The estimated k_2 rate constant in October was significantly greater ($P<0.01$) than in February. The reciprocal of the k_1 and k_2 rate constants is known as turnover time (Shipley and Clark, 1972). Thus, the addition of the turnover times of rumen and hind gut and the transit times of each individual animal (MTT) should be equal to MRT (Shipley and Clark, 1972). However, the MTT derived in this manner (Table 13) followed a similar

Table 13. Rate of passage by growing wapiti offered a pelleted ration during the period of October, 1976, to June, 1977.

	MONTH				
Parameter	Oct.	Dec.	Feb.	Apr.	Jun.
Mean Retention Time (h)	21.4^{a}	22.4^{ab}	28.7^{b}	24.1 [2]	28.1^{ab}
	(1.5) [1]	(1.5)	(1.5)	(1.9)	(1.9)
Transit Time (h)	6.94	6.04	6.89	-	6.64
	(0.60)	(0.60)	(0.60)	-	(0.77)
k_1 (h^{-1})	0.109^{mn}	0.154^{n}	0.0985^{m}	-	0.103^{mn}
	(0.014)	(0.014)	(0.014)	-	(0.018)
k_2 (h^{-1})	0.277^{a}	0.165^{ab}	0.140^{b}	-	0.183^{ab}
	(0.028)	(0.028)	(0.028)	-	(0.036)
Mean Turnover Time (h) (MTT) [3]	19.7	18.6	24.2	-	21.8

mn - when subscripts differ, the mean values are significantly different from each other ($P<0.05$). Duncan's New Multiple Range Test.

ab - when subscripts differ, the mean values are significantly different from each other ($P<0.01$). Same test as above.

[1] numbers in parenthesis are standard errors of the mean.

[2] value is estimated.

[3] the summation of the inverse of k_1 and k_2 and transit time.

pattern as MRT but lower in magnitude. The MTT value in February was also greater by 2.4 to 3.6 h than the values in October, December or June. The k_1 and k_2 values were not determined for April, since only two animals exhibited normal patterns of ^{103}Ru excretion discussed below.

Temperature had no effect on any of the parameters describing rate of passage.

Mean retention time was significantly related ($P<0.01$) to DM intake/$w^{.75}$. The following regression was derived and is illustrated in Figure 10:

$$\text{MRT (h)} = 38.68 - 0.16\ (\text{DM intake}, g/w^{.75}kg/d)$$

$$r = -0.417 \qquad \text{S.E.} = 0.06$$

Mean retention time was also significantly related ($P<0.01$) to DE intake/$w^{.75}$($r-0.420$), and digestible N intake/$w^{.75}$($r=-0.429$) but not to DM digestibility ($r=0.027$). Mean retention time was also significantly related ($P<0.01$) to body weight ($r=0.348$).

Recovery of the ^{103}Ru label was near 100% in animals, except wapiti 1135 in experiment 3, and wapiti 1133, 1137, 1134 and 1136 in experiment 4 (Table 14). The low recovery of ^{103}Ru from wapiti 1135 was the result of some being inadvertently lost during administration. In April, four wapiti (1133, 1134, 1136, 1137) were administered the ^{103}Ru dose using a shorter needle and the radioactive excretion pattern was similar to the pattern illustrated for wapiti 1137 in Figure 11. Twenty hours after the administration of the ^{103}Ru label, the concentration of ^{103}Ru was only 2000 cpm/g (Table 14). Very insignificant amounts, or no ^{103}Ru

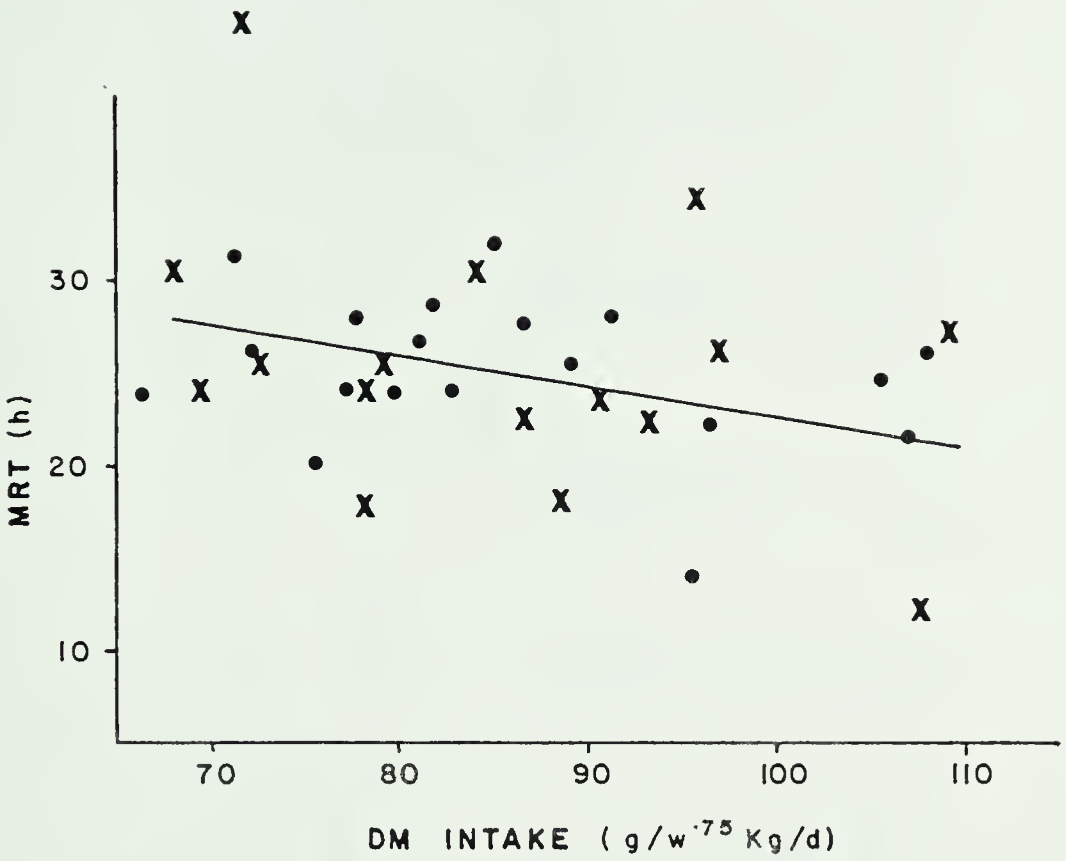

Figure 10. The relationship of DM intake with MRT.
MRT = 38.68 - 0.16 (DM intake) S.E. = 0.0604;
r = -0.415
(● = OUT wapiti; X = IN wapiti; MRT = mean retention time; DM = dry matter)

Table 14. Percent ^{103}Ru recovered in the feces of growing wapiti during digestion trials from October, 1976, to June 1977.

Experiment	Elk ID							
	1128	1133	1134	1135	1136	1137	1138	1139
Oct.	101.7	41.1	98.8	102.6	98.7	78.7	112.8	98.9
Dec.	83.7	119.7	99.7	99.5	98.9	90.0	90.3	102.6
Feb.	92.0	99.4	112.8	16.3	96.6	101.3	102.8	72.5
Apr.	101.8	42.6	29.8	-	27.7	32.3	90.1	-
Jun.	103.0	96.0	102.3	-	102.7	92.2	97.5	-

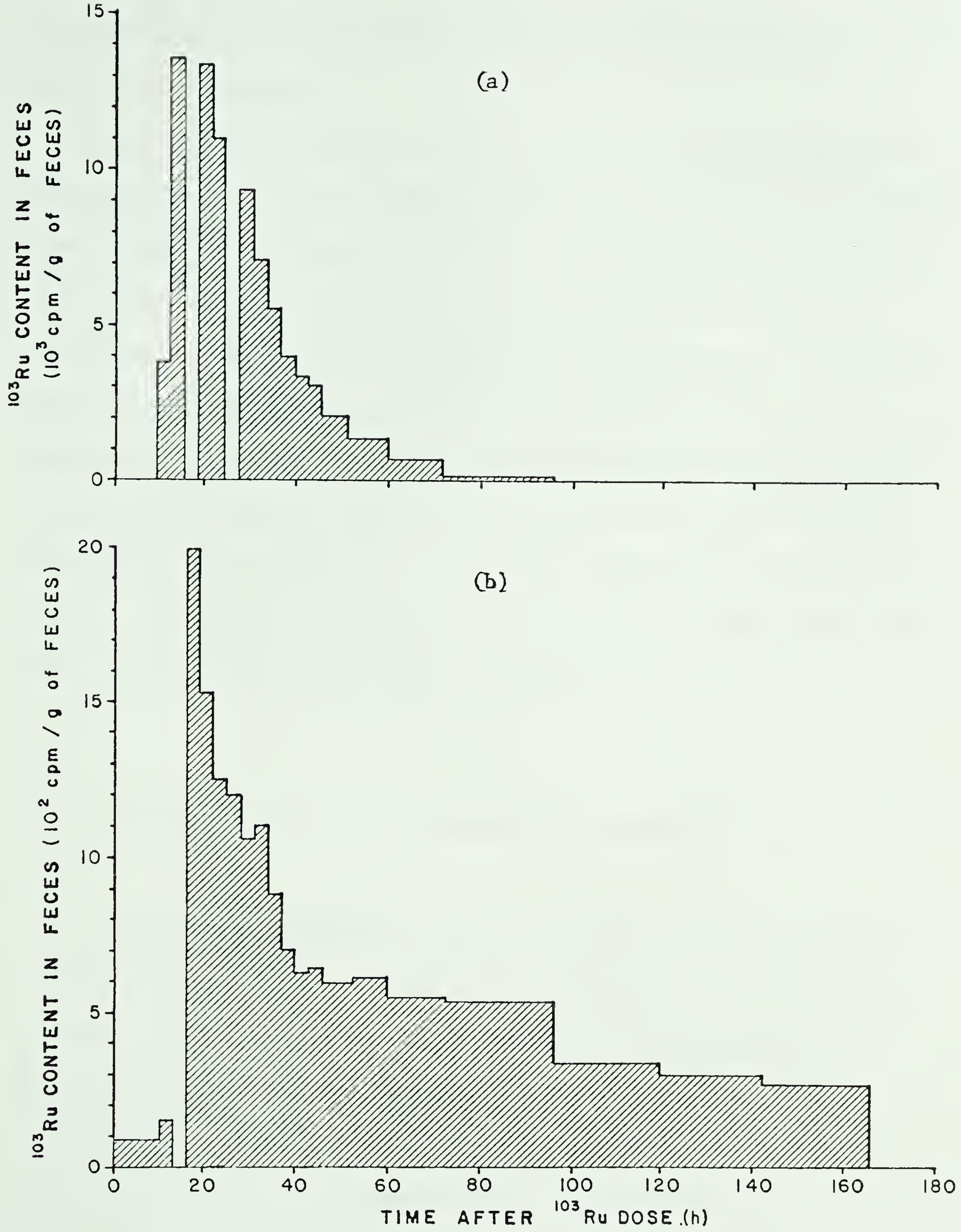

Figure 11. Radioisotope excretion pattern
(a) – normal excretion pattern of wapiti 1138
(b) – abnormal excretion pattern of wapiti 1137.

was detectable in the feces five to seven days after the administration of the radionucleotide.

In October and December, the ^{103}Ru label was administered orally, but in February, April and June the label was administered intraruminally (see Methods and Materials). In October wapiti 1138 and 1139 had MRT's of 13.0 and 12.1 h, respectively, and in December 13.8 and 18.0 h, respectively. These low MRT's suggested that the tracer was bypassing the rumen and, therefore, giving an estimate of the MRT in the post-ruminal gut. When the ^{103}Ru dose was administered into the rumen with an hypodermic needle and syringe, the radioactivity pattern from the succeeding fecal collections followed more closely the classical decay pattern illustrated in Figure 11a. MRT variation between animals was also significant ($P<0.025$) (Table 3, Appendix 5).

7.1.5. RELATIONSHIP OF THYROID HORMONES TO DIGESTION

Thyroxine was negatively related ($P<0.05$) to MRT, DM, E, N, fat and ADF digestibilities (r values were, respectively, -0.343, -0.456, -0.484, -0.491, -0.508 and -0.337), and T_3 was related negatively ($P<0.05$) to only N and fat digestibilities ($r=-0.404$ and -0.690, respectively). Thyroxine was also related ($P<0.01$) to DM, E and N intakes/$w^{.75}$ ($r=0.611$, 0.622 and 0.634, respectively).

7.1.6. URINE OUTPUT

Urine output when based on a water metabolic weight basis (to adjust for body weight) ($w^{.82}$) was not affected by either season or temperature. It was noted, nevertheless, that urine flow/$w^{.82}$ tended to decrease with season but not significantly ($P<0.05$). Water lost in the feces did not vary with season.

The IN wapiti had a higher % DM in the feces ($P<0.001$) than the OUT wapiti (33.7 and 30.7% for IN and OUT wapiti, respectively). Urine output by the IN wapiti tended to be higher than the urine output by the OUT wapiti, but failed to reach significance ($P>0.05$). Water intake (g/d) was highly related ($P<0.001$) to urine output ml/d ($r=0.777$) and total water loss (ml/d) ($r=0.774$). Urine collected over a 7 to 10 d period was also highly related to the urine collected and calculated over the 3 d period when the kinetics of urea-N was studied ($r=0.892$).

7.1.7. CRATE/PEN EFFECTS ON DIGESTION IN WAPITI

DM, P and Ca intake (g/d) of wapiti was lower ($P<0.01$) by 17% in the crate than in the pen. Water intake (ml/d) and total water intake intake/$w^{.82}$ (water in feed plus drinking water) was not affected by crate/pen effects. Digestibility of DM and N was 4% higher ($P<0.01$) in crates than in pens (Table 4, Appendix 4) and digestibility of P was about 17% higher ($P<0.025$) in the crate than in the pen. There were no crate-pen effects on the digestibility of fat, ADF, NDF, hemicellulose and Ca.

Observations of animals indicated that activity appeared to be greater in the pens than in the crates; more space was available in pens than in crates. Specific animals (wapiti 1134, 1138 and 1135) were often more restless in crates than the other wapiti.

7.2.0. DISCUSSION

The significant decrease in DM intake/$w^{.75}$ of wapiti in December, February and April, compared to October is a phenomenon that occurs widely in northern cervids (Wallmo et al., 1977) and also has been reported to occur in domestic sheep (Gordon, 1964). By late spring and early summer feed intake has increased and reaches a peak by mid-summer to early autumn. The wapiti did not show much of an increase in DM intake/$w^{.75}$ by June, although a slight increase was especially noted in the IN wapiti. Wapiti 1137 (IN wapiti) displayed increased mid-summer feed intake (g/d) during March, which indicated, besides pelage change and regressed antler growth, that it was out of phase with the outside photoperiod. The other IN wapiti (1133) did not have a marked DM intake during March. Similar changes in pelage and antler development observed in wapiti 1137 were observed in wapiti 1133 in late April although no marked increase in DM intake was observed. The antlers of wapiti 1133 did not show a similar state of maturity as wapiti 1137. If antler development in wapiti can serve as an indicator of photoperiod then this may suggest that wapiti 1133 and 1137 were sensing a prolonged spring-summer photoperiod. Goss (1977) demonstrated in sika deer (Cervus

nippon) that they retain their original antlers indefinitely when exposed to equational light cycles (12L : 12D), but when exposed to 13L : 11D the sika deer shed their antlers. Because the IN wapiti were exposed to a lower intensity of light during the day time than that compared to the OUT wapiti, the IN wapiti may have been responding to a mid-summer photoperiod when daylength is decreasing in reference to the length of dark cycle.

Although temperature had no significant effect ($P>0.05$) on DM intake/$w^{.75}$, it tended to be higher in the OUT wapiti than in the IN wapiti during October, December, April and June. Boll (1968) reported that captive wild wapiti tended to reduce DM consumption when ambient temperatures rose during winter, but found no significant changes in DM consumption as a result of temperature change. Ozoga and Gysel (1972), in discussion of their findings suggested that white-tailed deer reduced energy expenditure by slow walking, and selecting level land for their daily activity patterns. Thus, during periods of cold temperatures, less activity and bedding in sheltered areas may reduce the need for increased DM consumption when feed is both scarce and of lesser nutritional quality than that found in summer. Similar observations and conclusions were made by Flerov (1952) in roe deer of the USSR. In this study, the wapiti had a lower DM intake/$w^{.75}$ during the winter and spring months compared to that in October and may be related to a lowered resting metabolic rate which has been documented in reindeer and caribou (McEwan and Whitehead, 1970) and in white-tailed deer (Silver et al., 1969; Ullrey et al., 1970; Short, 1975).

Temperature change may have altered the behavior of the wapiti and contributed to the cyclical pattern of DM intake. Whenever late

fall storms occurred free-ranging wapiti were observed migrating to areas of increased shelter such as timber and sheltered valley floors (Dalke et al., 1965a). Harper (1971) observed wapiti to forage during the early and late afternoon hours on days with high temperatures and low humidity, and retreating into the timber during the heat of the day. On days that were cool and rainy, with high relative humidity, the wapiti were active and spent little time in the timber. However, as shown in this study, other factors appear to alter activity and DM intake, since the IN wapiti displayed similar activity and DM intake patterns as the OUT wapiti. The wapiti studied by Harper (1971) showed signs of anxiety and extreme restlessness and nervousness when barometric pressure was falling, whereas, during calm weather when barometric pressure was steady or rising, the wapiti foraged calmly, often covering a distance of about 35 m between bedding grounds. Similar observations were reported in red deer (Darling, 1963; Christie, 1967). Darling (1963) reported that red deer became more irritable as the air became more humid. The wapiti of this study were unable to migrate or seek sheltered areas, but they displayed irritability and restlessness before a drop in temperature occurred and simultaneously reduced feed intake. Other unexplained environmental forces may be acting upon the wapiti during weather changes, which requires further clarification.

The high correlation of DM intake and water intake in wapiti has similarly been reported in sheep and red deer (Maloiy et al., 1970). Siebert and Macfarlane (1969) found water turnover in cattle to increase as feed intake was increased. Cameron and Luick (1972) reported higher flux rates in reindeer during the spring and summer than during the winter season. Similar observations were made in deer and sheep

(Longhurst et al., 1970) and in cattle (Springell, 1968; Siebert and Macfarlane, 1969).

Macfarlane et al. (1967) have shown water intake to be directly related to salt intake in sheep. Siebert and Macfarlane (1969) and Springell (1968) have shown that cattle will also increase water turnover with increased protein intake. Cameron and Luick (1972) suggested that the seasonal changes in water turnover in reindeer may be related to the water content differences in the available plants between the summer and winter seasons. It appears from the data obtained in this study, that differences in water intake by the wapiti were not affected by salt intake, since the water intake to DM intake ratio (water/DM intake) remained relatively constant across seasons. However, temperature did affect water/DM intake: the IN wapiti had greater water intakes than the OUT wapiti very likely as a result of greater water flux. The IN wapiti tended to have greater urine output but also may have lost more water from body surfaces and by respiration than the OUT wapiti, similar to that observed in sheep (Joyce and Blaxter, 1964; Butcher, 1974) and other domestic ruminants (Macfarlane and Howard, 1972) exposed to warm environments, in contrast to animals exposed to cold environments.

Salt intakes recorded in this study were similar in wapiti calves reported by Boll (1968). He suggested that the salt consumption during this period was the result of novelty and not of necessity. Dalke et al. (1965a) studied range wapiti and reported that the salt grounds were visited by wapiti noticeably by mid-May and reached a peak during the second and third week of June, contrary to that found in captive growing wapiti. Seasonal patterns of salt intake for young growing wapiti may be different than observed in adults and needs further clari-

fication and study.

The increased digestibilities of DM, E, N, fat and NDF in the wapiti from October to June of the following year were similar to the observations reported in white-tailed deer (Holter et al., 1977).

The DE intakes in the wapiti were similar to those reported in reindeer and caribou (McEwan and Whitehead, 1970) and in white-tailed deer (Thompson et al., 1973; Holter et al., 1977). McEwan and Whitehead (1970) reported DE intake in reindeer and caribou of 1109 kJ/w$\cdot^{75}$d.

It also has been shown that a negative relationship of intake with digestibility occurred in sheep (Robertson and Van Soest, 1975) and in white-tailed deer (Ammann et al., 1973), which indicated the importance of holding feed intake constant to partition the effect of season and temperature on digestibility and MRT. However a poor correlation of DM intake/w$\cdot^{75}$ with digestibility was obtained in the wapiti indicating that other factors may be involved. Mean retention time was significantly related ($P<0.01$) to DE intake/w$\cdot^{75}$($r = -0.420$), but not to DM digestibility ($r = 0.027$), as reported in sheep by Westra and Christopherson (1976) and Kennedy et al. (1977). The seasonal digestibility pattern in white-tailed deer. Holter et al. (1977) reported a general decline in digestibility of ADF from early winter to late fall in the same year; the digestibility coefficients of ADF were over 50% lower in white-tailed deer than the coefficients determined in the wapiti.

The reduction in digestibility of E and ADF in wapiti exposed to outside temperatures compared to wapiti exposed to a constant temperature of 18 to 19 C is consistent with that found in shorn sheep under similar experimental conditions (Westra, 1975). Other investigators have reported reductions in digestibility of DM in sheep and cattle exposed to

cold temperatures (Graham et al., 1959; Blaxter and Wainman, 1961; Bailey, 1964; Graham, 1964). This phenomenon has been shown to be physiologically controlled (Westra and Christopherson, 1976; Thompson et al., 1978) and not as a result of differences in fermentation rates of feces within cold treatments (Fuller and Cadenhead, 1969). The digestibility of N in wapiti was affected by temperature, contrary to that reported in shorn sheep (Westra and Christopherson, 1976; Kennedy et al., 1976). In April, the digestibility of N and the digestibility of most of the other nutrient components tended to be higher in the OUT wapiti than in the IN wapiti and may have been a response by the OUT wapiti to higher temperatures compared to the low temperatures just prior to the experiments.

In relation to fiber digestion, Mertens (1977) divided rumen digestion into four components: digestion rate, digestion lag, potential extent of digestion and passage rate. The apparent extent of digestion is affected by each of these components and these components may be influenced by factors such as the morphology and physical nature of the fiber, as well as, by other influencing agents, as Mertens (1977) suggested, that "inhibit or stimulate rumen microbial growth and their fiber-degrading enzymes". Mertens (1977) further suggested that digestion lag may be influenced by such agents as microbial populations, the attachment of microbes to fiber prior to digestion and/or the physical and chemical alteration of fiber before microbial digestion can occur. Thus differential digestion may occur between the less fermented forms of glucose polymers in cellulose and the more readily fermented forms of glucose polymers in the starches and dextrins and various forms of simple sugars (molasses). These factors, digestion lag and rate of

digestion, are, however, greatly influenced by MRT of digesta in the rumen (Johnson, 1976). MRT, as estimated by the residence time of a radioactive marker in the digestive tract, has been shown to be indirectly related to reticulum motility (Westra, 1975). In addition, reticulum motility in shorn sheep exposed to cold (1 C) was significantly greater than that in sheep exposed to warm (21 C) environments (Westra, 1975). These observations may explain the fall in digestibility of ADF and the increased k_1 value in wapiti during the colder months of December and February compared to October, April and June, while the digestibility of the more easily digested forms of feed (DM, N, E, fat and NDF) remained relatively stable or increased with time. Compared to that in October, the greater k_1 value in December suggested that the feed spent less time in the rumen. There was also simultaneous decrease in the k_2 value which meant an increase in turnover time in the hind gut. This may explain the increased digestibilities of many of the nutritive components (except ADF) in December compared to October. In February, despite the decreased k_1 value of 1.5 times that in December, the digestibility of ADF tended to rise only slightly. However, in June the digestibility of ADF was similar to that in October, and so were the k_1 values. The k_2 value in June was 1.5 times smaller than in October, and the digestibilities of DM, E, N and fat were greater in June than those in October. This suggested that the more readily digested components resided in the hind gut longer in December, February and June than in October and, therefore, may explain the reason for these digestibility coefficients rising during the period of December to June.

The MRT of the pelleted ration estimated by the ^{103}Ru marker in wapiti was higher than the MRT of a pelleted ration estimated in white-

tailed deer (14 h), using $^{51}CrCl_3$ as a digesta marker (Mautz and Petrides, 1971). Mean retention times ranged from 13.7 h in one deer to 17.1 h in another deer. The differences in MRT between white-tailed deer and wapiti may be consistent with the differences in the rations of rumen volume to body weight between species (Hofman, 1973; Nelson and Leege, 1978). More work is necessary to confirm these suggested differences.

Mautz and Petrides (1971) found large variations in MRT among deer, similar to that found in the wapiti of the study. In October and December the low MRT of wapiti 1138 and 1139 may have been due to very little or no mixing of the label in the rumen before entering the postruminal digestive tract. The differences between MRT and rate of passage may have been due to a combined variation of the differences between the methods of derivation and the differences in patterns of excretion of the label between animals. More work is needed in wild ungulates to understand the causes of variation in MRT.

Injection of the label intraruminally gave normal excretion patterns, except in April. The abnormal excretion patterns in April may have been due to the contamination of the feces by urine containing ^{103}Ru. When an identical Ru-complex was injected into the peritoneal cavity of rats it was quickly excreted into the urine. The Ru-complex was also reported to be nontoxic and failed to accumulate in the tissues except the kidney and liver (Koch et al., 1957). It was assumed that a similar activity occurred in four of the wapiti in April as a result of inadvertently injecting part of the label into the peritoneal cavity.

Thorne and Butler (1976) calculated the time it took for 90% of the marker (sanfranin O) to be excreted by wapiti consuming rations of different forms. The reported rates of passage were 60 to 80 h for a

pelleted ration, and 120 to 130 h for a baled hay ration. The time it took for passing nearly all the ^{103}Ru from the digestive tract in the wapiti of this study ranged between 5 and 7 days, similar to that determined in red deer and fallow deer offered a granulated grain mixture (Lochman et al., 1973). Lochman et al. (1973) determined rate of passage by using tree bark as a marker. They determined the time it took for 95% of the marker to disappear (actual) and the time no more indicator was observed in the feces (total). Red deer and fallow deer offered a ration of alfalfa had actual and total times of 4 and 6 days respectively; on a ration of dried leaves the actual and total times were 7 and 12 days; and on a ration of granulated grain mixture specifically mixed for antler development the actual and total times were 3 to 4 and 6 to 8 days, respectively. Rates of passage derived in this manner (tree bark) tended to be lower by 1 to 2 days for roe deer.

Mean retention time has been shown to be significantly related to T_3 and T_4 in sheep. Kennedy et al. (1977) demonstrated that either injections of T_3 (0.25 mg/d) and/or cold exposure (2 to 5 C) significantly reduced DM digestibility and increased metabolic activity as measured by indirect calorimetry. In wapiti, T_4 was related more highly to MRT and digestibility than was T_3. Intake/$w^{.75}$ of DM, E and N were related to T_3 and T_4. Similar results have been reported in goats (Abdullah and Falconer, 1977) and cattle (Miller et al., 1974). Seal et al. (1972b) found T_4 to be significantly reduced in white-tailed deer on a low plane of nutrition compared to deer on a high plane. Ingram and Kaciuba-Uscilko (1977) concluded from their work with pigs that the increased E intakes significantly increased the utilization rate of ^{125}I thyroxine, but that low temperatures and food bulk had no effect.

In the wapiti of this study, intake/w$^{.75}$ was more related to serum T_4 and T_3 concentrations than it was to either MRT or the digestibility coefficients. The work of Ammann et al. (1973) suggested that white-tailed deer were able to adjust DM intake of varying digestibility to maintain a constant energy balance close to maintenance requirements. However when digestibile E in the ration was reduced below a minimum of 9.08 kJ/g maintenance energy intake could no longer be maintained due to the threshold capacity of digestive tract fill. The interaction of thyroid activity and energy intake may exist as a fine control of metabolic rate.

It also was found that T_3 and T_4 were significantly ($P<0.01$) and negatively related to body weight—a criterion confounded with age. Yousef and Luick (1970) concluded that season had no effect on thyroxine kinetics, but that biokinetic activity of thyroxine decreased markedly with age (see discussion of 6.1.8.). Nevertheless, high serum T_4 and T_3 concentrations during the growth phase may not only be necessary for intestinal maturation (Thompson et al., 1973) and bone development (see discussion 6.1.8.) but a lower MRT may be beneficial for quickly passing feeds of high solubility and low fiber content to meet maintenance and growth requirements. In winter growth of young wild ungulates is usually static (McEwan, 1977) and a reduction in maintenance costs would be beneficial when good quality feed is scarce. Hoffman and Robinson (1966) found in deer less active thyroids in winter than in summer and suggested that deer in winter may have lower metabolic rates than in summer. This was later confirmed in white-tailed deer (Silver et al., 1969) and in caribou (McEwan, 1970). Therefore during the winter when both availability and digestibility of feed is low, it

may be more advantageous for wapiti to conserve energy by maintaining a lower metabolic rate, reducing daily activity in the search for greater volumes of feed (Ozoga and Verme, 1970) and increasing MRT in an attempt to increase the digestibility of DM, N, E, NDF and fat. In addition, when ambient tamperatures in winter decrease it then may be more advantageous to reduce rumen retention time in an attempt to increase the availability of more digestible components to hind gut digestion which escape rumen digestion, as well as increase the efficiency of microbial synthesis in the rumen (Kennedy and Milligan, 1978).

There has been some evidence that crate effects may contribute to variation of digestion in wild ruminants. Mautz (1971) reported that digestibility of DM declined markedly in the 2 white-tailed deer after they were transferred to a crate. Dry matter intake(g/d) in one deer increased but in the second deer it decreased and did not return to pre-confinement levels after 9 to 12 days. Phar _et al_. (1970) found no differences in nutrient digestibilities in cattle after a conditioning period of 12 to 19 days. The crate-pen effect on nutrient intake and digestibility in the wapiti indicated that the period of adjustment to the crates may not have been sufficiently long. However, the activity differences of wapiti between pen and crate may have contributed an equal or greater amount of variation.

CHAPTER 8

EFFECT OF SEASON AND TEMPERATURE ON NITROGEN UTILIZATION

Urea recycling contributes significantly to the nitrogen economy of ruminants and is an important means by which N is conserved when N intake is decreased. Urea recycling in young growing cervids in the first year of life may be an important mechanism for conserving N during times when the potential for growth is the highest and when extreme environmental conditions occur. Weight losses are common in winter McEwan, 1972) and it, therefore, would seem logical that N recycling might be high. Work has been done in urea kinetics of wild ungulate offered various levels of protein in the ration (Wales, 1972; Robbins *et al.*, 1974; Kirkpatrick *et al.*, 1975; Hove and Jacobson, 1975). Wales (1972) found that adult caribou recycle significantly greater amounts of urea in winter than in summer. N intake by the caribou during the winter was voluntarily reduced from the summer by 35.7%. However, during the winter period the absolute amount of N in the feed varied because of the different proportions of lichen (2% protein) and a pelleted ration (12% protein). In addition, the solubility of the protein in each of the N sources may have also been different. It has been well documented that wild ruminants reduce feed intake during the winter season compared to the other seasons, particularly in late summer, and that feed quality is also diminshed during the winter season. However, Robbins *et al.*(1974) has shown that urea recycling in growing white-tailed deer was indirectly affected by the amounts of N consumed. No investigations have been designed to date, to determine

if season *per se* (photoperiod and age) has a significant effect on urea recycling in wild ruminants.

Investigations into the ability of wild ruminants to recycle urea under different temperature exposures has been studied very little. Kennedy and Milligan (1978) reported that cold-exposed sheep (2 - 5 C) have a greater transfer of plasma urea to the rumen ammonia pool, determined by a ^{15}N marker. They also reported a greater proportion of bacterial N was derived from ammonia in cold-exposed sheep compared to warm-exposed sheep.

The design of the present study afforded an opportunity to investigate the effects of both temperature and season on urea utilization in growing wapiti.

8.1.0. METHODS AND MATERIALS

The urea pool of each wapiti was labelled with a single injection of approximately 10 μCi of ^{14}C-urea via the jugular vein immediately after obtaining a plasma and serum blood sample. Ten to 15 cm of catheter tubing was fitted between a 10-ml sterile syringe, which contained the ^{14}C-urea dose, and a 22 guage hypodermic needle so that the risk of the needle coming out of the vein after its insertion was minimized. The ^{14}C-urea was made up in 0.15 M NaCl solution at a concentration of 1 μCi/ml of saline. The single dose was administered between 1200 and 1300 h.

Urine was collected and measured by volume every 1 to 2 hours for the first 10 hours after the ^{14}C-urea administration and then once every 3 hours for the next 36 hours. Subsequent urine collections were made at

increasingly extended intervals of 6, 20 and 24 hours for the remainder of the trial. To be confident that the collection of the label in the urine was complete and to provide a constant time period on which to base urea excretion rate, a trial length of 52 h was chosen. It was found that 75 to 90% of the label was excreted after the first 12 h.

A 10 ml sample and a second sample, which consisted of a 5% aliquot of each urine collection was saved, and frozen for later analyses. Urine urea-N concentration was determined in duplicate by an automated modification of the diacetyl monoxamine reaction (Technicon Auto Analyzer file N-10a). Urine ^{14}C radioactivity was determined by mixing 0.4 ml of urine, and 0.4 ml of distilled water with 15 ml of Aquasol-2, Universal L.S.C. Cocktail (New England Nuclear). The distilled water dispelled any cloudiness that occurred in the mixture. The samples were counted in a Mark III Liquid Scintillation System (Model 6850, Searle Analytic Inc. Ill.) for 10 minutes, with a counting efficiency of approximately 85%.

The technique used to estimate urea-N entering the digestive tract was developed by Ford (1969) at the University of Alberta. This technique assumed that if animals were maintained on a steady fed state, then the urea influx to the body pool equalled efflux. The major exits of urea would be via the urine and the transfer from the blood plasma to the digestive tract where urea hydrolysis occurs. Therefore, the equation used to estimate urea recycling was:

$$R = \frac{1 - L}{L} \times U$$

Where: R = grams of urea recycled per day

U = grams of urea excreted in the urine per day

L = the fraction of injected label recovered in the urine

It was assumed that rumen ammonia and plasma urea-N fluctuations remained relatively small when feed was offered on an *ad libitum* basis. It was observed that the wapiti of this study, normally fed during the morning and late afternoon hours and consumed feed often and in small amounts. In addition, since all animals were given the ^{14}C-urea at approximately the same time each time it was administered, it was assumed that the total percent of the label excreted would provide an accurate estimate of the differences in recycling of the label between seasons and temperature treatments. Although Hove and Jacobsen (1975) noted that reindeer exhibited lower blood-urea N levels during the night than during the daytime when fed high N rations twice daily, Lewis (1957) noted that blood-urea levels in sheep exhibited little diurnal variation. Maloiy *et al*. (1970) observed that when red deer and sheep were offered a high N diet twice daily, a moderate increase in rumen ammonia concentrations occurred after each meal, with only minor and irregular fluctuations of plasma urea during the day.

Therefore, urea flux could be estimated by calculating the summation of urea recycled and urea excreted. Flux is an estimate of the urea leaving the urea pool of the animal per unit time (Ford, 1969).

Nitrogen retention was calculated as follows:

$$N\ ret = Nint - (NF + NU)$$

Where: N ret = nitrogen retained (g/d)

Nint = nitrogen intake (g/d)

NF = nitrogen in feces (g/d)

NU = nitrogen in urine (g/d).

Urea clearance rates were determined using the relationship (Levinsky and Levy, 1973):

$$\text{Clearance} = \text{UV} \times \frac{\text{Uu}}{\text{Pu}}$$

where:

Clearance = urea cleared from plasma by kidney per unit time (ml/min)

UV = urine volume excreted per d (ml/min)

Uu = urine urea concentration (mg/ml)

Pu = plasma urea concentration (mg/ml)

8.2.0. RESULTS

. . UREA-N KINETICS

Many of the urea-N parameters were affected by season, but not by temperature (Figure 12). Urea-N recycled/$w^{\cdot 75}$ to the digestive tract and urea-N flux/$w^{\cdot 75}$ were significantly ($P<0.01$) affected by season (Figure 12). The wapiti recycled more than twice the urea-N in October than in December and February (coldest months)when digestible N(DN) intake was reduced in the latter two months from October by 8.7 and 18.5%

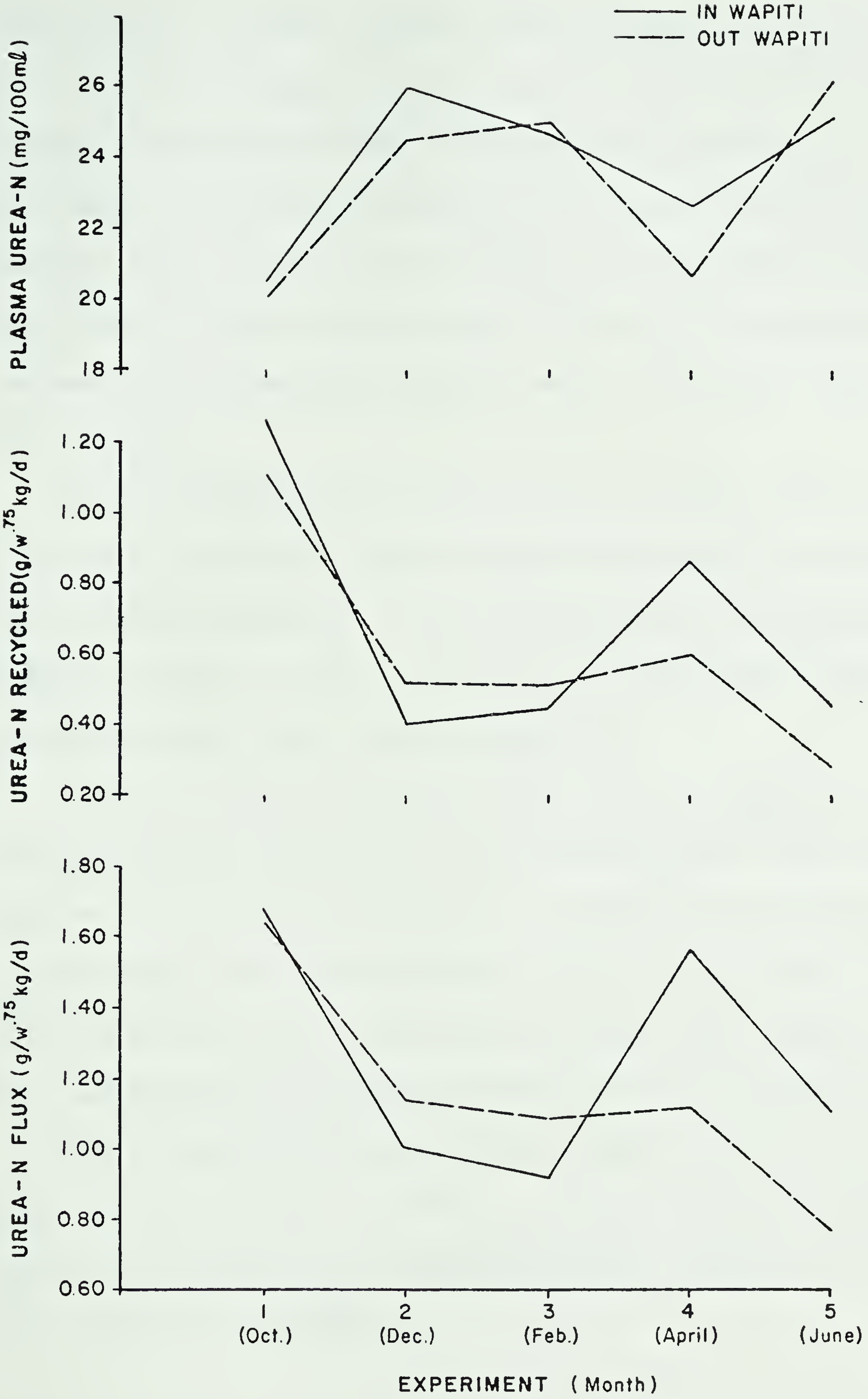

Figure 12. The effect of season and temperature on plasma urea-N (mg%), urea-N recycled ($g/w\cdot^{75}kg/d$) and urea-N flux ($g/w\cdot^{75}kg/d$).

respectively. In April, recycled urea-N increased, with the IN wapiti tending to have greater recycling of urea-N than the OUT wapiti; although the differences were not statistically significant.

DN intake in October was significantly greater ($P<0.05$) than in February, April and June and in December , it was greater ($P<0.05$), than in April (Figure 13). The urea-N excreted/$w^{.75}$ remained relatively constant across experiments (overall mean = 0.56 g/$w^{.75}$ kg/d; S.E. = 0.026).

PUN was significantly lower ($P<0.01$) in October than in the other months, except in April, which was between the values of October and the other 3 months (Figure 12). Urea-N recycled/$w^{.75}$ was negatively related ($P<0.01$) to PUN ($r = 0.442$). Urine urea-N concentration remained relatively stable across seasons (Table 12).

Percent ^{14}C label recovered in the urine was significantly lower ($P<0.01$) in October than any of the following months (Table 15). Recoveries of ^{14}C label in the urine in December and February were similar and were significantly higher than in April. In June, the ^{14}C recovery in the urine was twice that in October, which suggested that in June less urea-N was available for recycling to the digestive tract.

Urea-N cleared per unit metabolic weight, remained relatively stable in all experiments (Table 15). Urea-N excreted expressed as a percent of N excreted also remained relatively constant in all experiments (48.3%; S.E. = 1.62%).

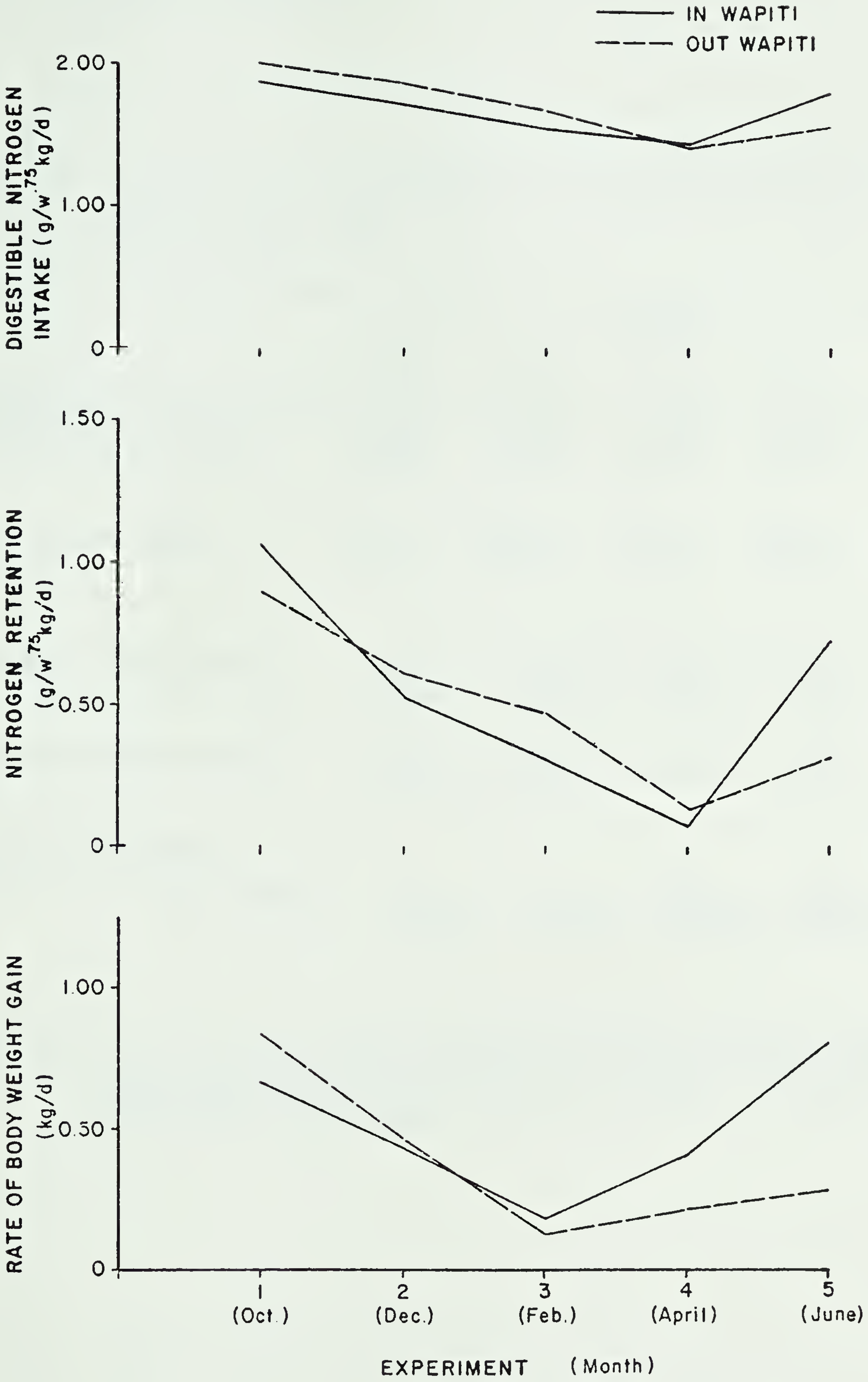

Figure 13. The effect of season and temperature on digestible N intake, N retention and rate of body weight gain.

Table 15. Urea-N kinetics determined in growing wapiti from October, 1976, to June, 1977.

	MONTH				
Parameter	Oct.	Dec.	Feb.	Apr.	Jun.
N Intake (g/w$^{.75}$kg/d)	2.89^{a} (0.09)	2.49^{b} (0.09)	2.25^{bc} (0.09)	1.91^{c} (0.12)	2.23^{bc} (0.12)
Urine urea-N (mg%)	437 (3.47)	552 (3.47)	465 (3.47)	548 (4.48)	567 (4.48)
% label ^{14}C recovered	33.9^{a} (2.04)	57.2^{cd} (2.04)	53.9^{c} (2.04)	45.2^{b} (2.62)	65.6^{d} (2.62)
Urea-N excreted (g/d)	14.7^{a} (1.97)	21.1^{ab} (1.97)	21.3^{ab} (1.97)	29.5^{b} (2.55)	29.2^{b} (2.55)
Urea-N clearance (l/w$^{.75}$kg/d)	2.59 (0.208)	2.44 (0.208)	2.06 (0.208)	2.75 (0.269)	2.19 (0.269)

abcd – when subscripts differ within rows the mean values are significantly different from zero ($P<0.01$). Duncan's New Multiple Range Test.

8.2.2. NITROGEN RETENTION

Nitrogen retained ($g/w^{.75}kg/d$) was significantly ($P<0.025$) affected by season and had a significant ($P<0.005$) season and temperature interaction (Figure 13). In October, N retention/$w^{.75}$ was significantly greater ($P<0.01$) than in any of the following months, and in April, it was the lowest ($P<0.01$). N retention/$w^{.75}$ was reduced in December and February (coldest months) by 27.6 and 43.1% , respectively, compared to that in October. Between temperature treatments N retention/$w^{.75}$ did not differ, except in June when N retention/$w^{.75}$ was significantly greater ($P<0.01$) in the IN wapiti than in the OUT wapiti. The rate of gain was significantly correlated ($P<0.01$) to N retention/$w^{.75}$ ($r = 0.573$; S.E. = 0.36). Body weight gain between the IN and OUT wapiti did not differ within months, except in June, when the IN wapiti had a significantly greater ($P<0.01$) body weight gain than the OUT wapiti (Figure 13).

Digestible N followed a similar pattern as N retention/$w^{.75}$ and body weight gain but the seasonal peaks were more highly attenuated. In October, DN intake was greater ($P<0.01$) than that in February, April or June, and in December, it was greater ($P<0.01$) than that in April (Figure 13).

8.2.3. NITROGEN REGRESSIONS AND CORRELATIONS

Urea-N excretion (g/d) was significantly related ($P<0.01$) to nitrogen intake (g/d), urinary N excreted (g/d), urine excretion rate

(ml/d) and water intake (ml/d). The regression equations calculated are as follows:

$$\mathrm{Urex} = -4.41 + 0.283\ \mathrm{Nint} \qquad r = 0.688 \qquad \mathrm{S.E.} = 0.051 \qquad (6)$$

$$= 4.99 + 0.355\ \mathrm{Nx} \qquad r = 0.775 \qquad \mathrm{S.E.} = 0.050 \qquad (7)$$

$$= 8.52 + 0.00302\ \mathrm{Ux} \qquad r = 0.526 \qquad \mathrm{S.E.} = 0.0084 \qquad (8)$$

$$= 1.36 + 0.00188\ \mathrm{Wint} \qquad r = 0.699 \qquad \mathrm{S.E.} = 0.00033 \qquad (9)$$

Where: Urex is urea-N excretion (g/d)
Nint is N intake (g/d)
Nx is N excreted (g/d)
Ux is urine excretion rate (ml/d)
and Wint is water intake (ml/d)

When N intake (g/d) and water intake (ml/d) were regressed on urea-N excretion (g/d), they contributed 58% of the variation ($P<0.001$).

$$\mathrm{Urex} = -6.04 + 0.165\ \mathrm{Nint} + 0.0012\ \mathrm{Wint}$$

$$r = 0.760 \qquad \mathrm{S.E.} = 4.6 \qquad (10)$$

Urea-N recycled (g/d) was related to PUN ($P<0.05$) and highly related to urea-N flux (g/d) ($P<0.001$). The following regression equation was derived:

$$\mathrm{Urrc} = 54.65 - 1.36\ \mathrm{PUN} \qquad r = 0.331 \qquad \mathrm{S.E.} = 0.667 \qquad (11)$$

where: Urrc = urea-N recycled (g/d)
PUN = plasma urea-N (mg%)

Urea-N flux (g/d) regressed on urea-N excreted (g/d) was also significant ($P<0.01$).

$$\text{Urrex} = 10.68 + 0.245 \qquad r = 0.591 \qquad \text{S.E.} = 0.057 \qquad (12)$$

Urea-N flux/$w^{.75}$ and urea-N recycled/$w^{.75}$ was related ($P<0.01$) to N intake ($r = 0.460$ and 0.476 respectively). Total water intake/$w^{.82}$ also was significantly related to urea-N flux/$w^{.75}$ and urea-N recycled/$w^{.75}$ ($r = 575$ and 0.587 respectively). The relationship of water intake/$w^{.82}$ and PUN ($r = 0.20$) was not significant ($P>0.05$).

Urea-N clearance (1/d) was significantly ($P<0.01$) related to N intake (1/d), urea-N excreted (g/d) and urea-N flux (g/d) and the following equations were derived:

$$\begin{aligned} \text{UCL} &= -4.23 + 1.04\ \text{Nint} && r = 0.603 && \text{S.E.} = 0.051 && (13)\\ &= 9.85 + 3.79\ \text{Urex} && r = 0.901 && \text{S.E.} = 0.313 && (14)\\ &= 38.41 + 1.20\ \text{Ufl} && r = 0.687 && \text{S.E.} = 0.217 && (15) \end{aligned}$$

where: UCl = urea-N clearance (1/d)

Equations 13 and 14 are graphically depicted in Figure 14.

When N intake (g/d) and water intake (ml/d) were regressed on urea-N clearance (1/d) they contributed 48% of the variation ($P<0.01$).

$$\text{UCl} = -11.42 + 0.52\ \text{Nint} + 0.0051\ \text{Wint} \qquad (16)$$

$$r = 0.693 \qquad \text{S.E.} = 21.4$$

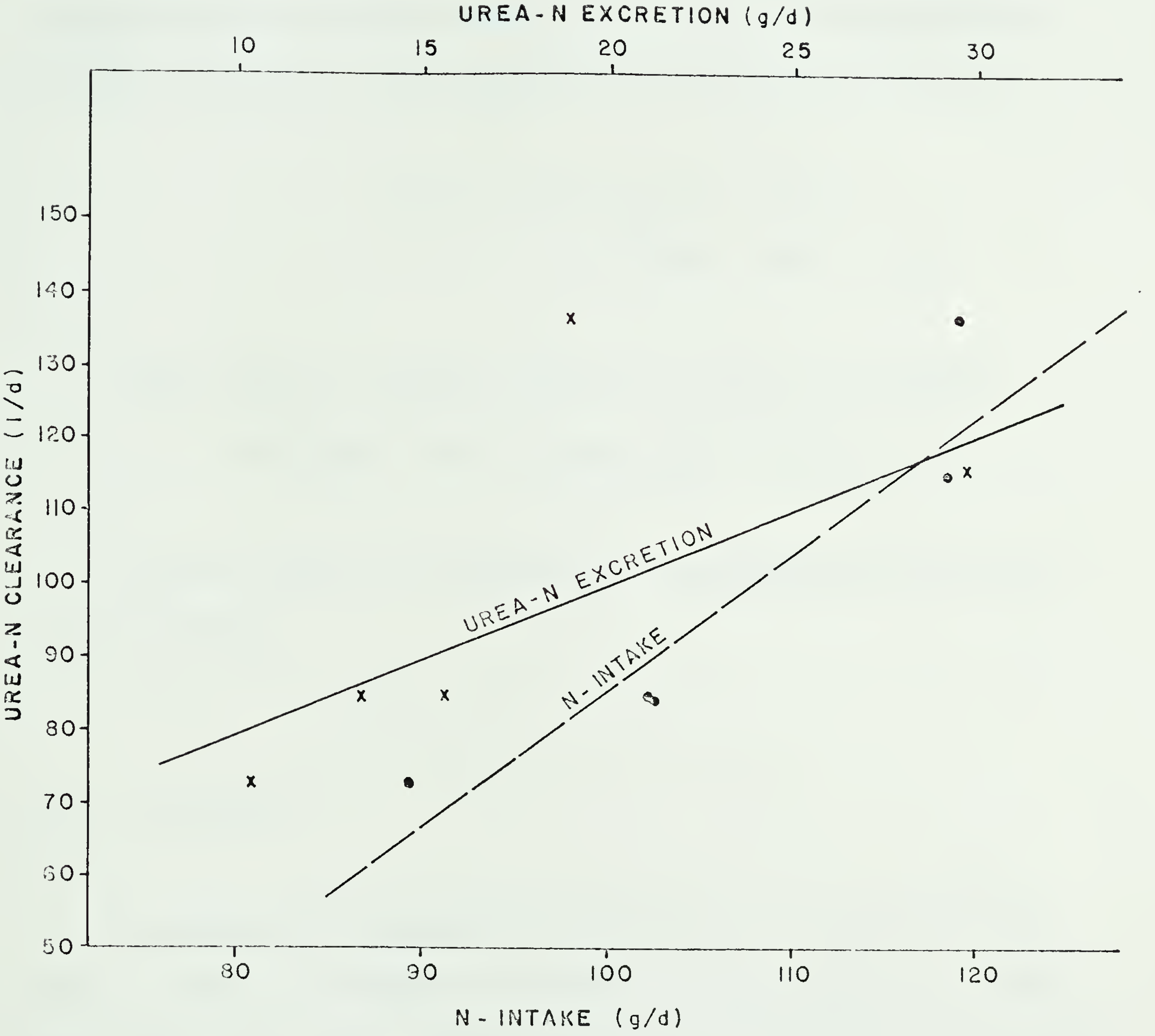

Figure 14. The relationship of N intake (g/d) and urea-N excretion (g/d) with urea-N clearance (g/d).
Urea-N clearance = −4.23 + 1.04 (N − intake) S.E. = 0.51

= 9.85 + 3.79 (urea-N excretion) S.E. = 0.313

The plotted points are the overall means obtained within each of the five months determined; ie., October, December, February, April and June.

● = N intake; x = urea-N excretion.

Shown in Figure 16 is the regression of digestible N/$w^{.75}$ on nitrogen retention/$w^{.75}$ for wapiti throughout the winter. Despite the fact that the validity of balance trials to estimate nitrogen requirements in animals is questionable (Duncan, 1958), it has been generally accepted that it provides a means for estimating the efficiency of nutrient utilization. The regression was described as follows:

$$\text{N Ret} = 1.019\ (\text{Dig N}) - 1.200$$

$$r = 0.800 \qquad \text{S.E.} = 0.131$$

where: Dig N = apparent digestible nitrogen (g/$w^{.75}$kg/d)

and N Ret = the N retained (g/$w^{.75}$kg/d).

Thus the amount of N required for N equilibrium in wapiti was 1.362 g/$w^{.75}$kg/d.

8.3.0. DISCUSSION

The amount of N required for maintenance in the wapiti was nearly 3 times that required for reindeer, caribou (McEwan and Whitehead, 1970) and sheep (Brody, 1945; Harris and Mitchell, 1941; Moir and Williams, 1950), and 6 to 7 times greater than those reported for sheep by other investigators (Elliot and Topps, 1964; Robinson and Forbes 1966). Elliott and Topps (1964) have demonstrated that by increasing the proportions of ground roughages in the ration it also increased the N requirements for N equilibrium. This may be the reason why the wapiti of this study had high maintenance requirements for N. Animal age

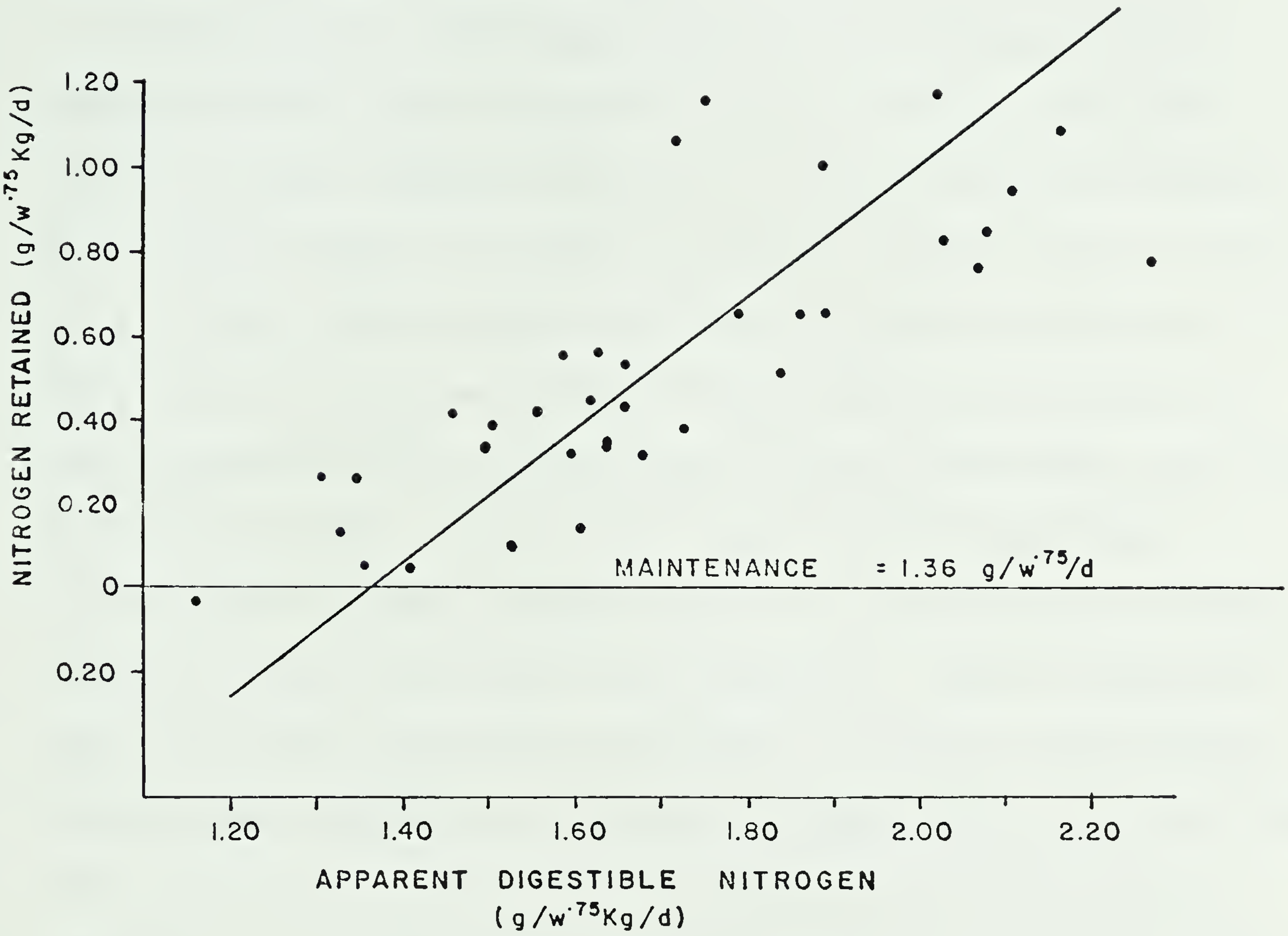

Figure 15. The relationship of apparent digestible nitrogen (Dig N) with nitrogen retained (N Ret).

N Ret = 1.019(Dig N) - 1.200 S.E. = 0.131 r = 0.800

* The effect of age is confounded within this relationship.

effects may have biased the maintenance requiremnnts upward, although no evidence is presently available to indicate this. The N maintenance requirement in growing animals was assumed to be the amount of DN intake required for growth to remain static.

The amount of urea-N recycled in wapiti was within the range reported by Ford (1969) in sheep ($\bar{x}$ = 0.55 g/w$^{.75}$kg/d) and by Wales (1972) in caribou during the summer ($\bar{x}$ = 0.44 g/w$^{.75}$kg/d) and winter ($\bar{x}$ = 0.65 g/w$^{.75}$kg/d). The sheep and caribou, however, were fed on a lower N intake. When recycled urea-N was calculated as a percent of the N intake, the caribou studied by Wales (1972) had percentages of 30% in summer and 69% in winter whereas the beef bulls (Wales, 1972) had a percentage of 33%. In this study, recycled urea-N (expressed as a percent of the N intake) amounted to 53, 25, 21, 29 and 13% for October, December, February, April and June, respectively. When DN intakes are high, N recycled is expected to be reduced. In April, urea-N recycled increased when expressed as a percent of N intake (29%), which may account for a greater need of N for new hair growth, but also may have been a response to a lower DN intake and a lower N retention compared to the previous months. A reduced DN intake may have also been a response to higher temperatures during the time when the winter hair coat was being shed, but this explanation is doubtful, since the IN wapiti showed parallel changes in DN intake and growth rate. Robbins (1973) reported that in white-tailed deer the average N and E requirements for hair was approximately 0.09 g/w$^{.75}$kg/d and 13 to 17 kJ/w$^{.75}$kg/d, respectively. Assuming that N requirement for growth of hair in wapiti was similar to that in white-tailed deer, then only 9.2% of the N retained in October may be attributed to hair growth, whereas, 70.3% of the N retained in

April may be attributed to hair growth. The low proportion of the N retained for hair growth in October does not explain the observed high N retention in that month. In April, it is tempting to explain that the low N rentention may be due to exceptionally warm temperatures, as suggested by Fuller (1965) in pigs and by Holter et al. (1977) in white-tailed deer. But as indicated above, the IN wapiti showed parallel changes in N retention to the OUT wapiti. Therefore temperature does not appear to be a factor; besides, the IN wapiti were already in or nearly in their summer pelage in April. Greater N retention by the IN wapiti than by the OUT wapiti in June, suggested that wapiti in summer not only may have a higher metabolic rate, assuming they are similar to white-tailed deer (Silver et al., 1969; Holter et al., 1975), reindeer and caribou (McEwan and Whitehead, 1970), but may be more efficient in storing protein and energy in summer than in winter, similar to rodents before hibernation (Pengelley, 1965). Kochakian (1960) has shown that testosterone and other steroids markedly depress N excretion and increase protein deposition in pigs. Testosterone is necessary for the synthesis of the antler matrix (Bubenik et al., 1974) and is associated with the drying of antler velvet. This may explain why the IN wapiti had greater N retention in June than the OUT wapiti. In October, the aggressive behavior of the IN and OUT wapiti (Chapter 5) may be associated with an increased production of testosterone (Kennaugh et al., 1977) which has been shown to rise in the plasma of well fed red deer at the age of three months (Chapman, 1975). This aggressive behavior observed in September and October may explain the high N retention observed during October. In adult animals, testosterone production begins to increase in early summer and peaks at the beginning

of the rut or soon after (Chapman, 1975) the period of time when weight gain is highest. Caillol and Martinet (1976) demonstrated in field voles (Microtus arvalis) that long daylight hours, as opposed to short daylight hours, increased the proportion of nitrogen metabolized which resulted in a subsequent increased rate of growth. This suggests that seasonal differences in N retention and urea-N recycling may occur as a result of photoperiod and not entirely to age of the animal. Photoperiod may be an important cue to growing wapiti for altering its hormonal status (Mirarchi et al., 1978) which in turn may affect the digestive efficiency for storage of energy and protein in growth and body weight gain. Thyroid hormones have been demonstrated to contribute to changes in digestive function of the rumen; i.e. T_3 was directly related to rumen motility (Westra and Christopherson, 1976) and rate of passage of digesta (Kennedy et al., 1977). In winter when food supply is limited it also may be advantageous to turn down metabolic activity so that maintenance requirements are met, similar to that observed in small birds and poikilotherms in response to cold temperatures (Fry, 1958). Lower resting metabolic rates in winter compared to that in summer have been reported in white-tailed deer (Silver et al., 1969), reindeer and caribou (McEwan and Whitehead, 1970). However, unlike small birds and poikilotherms, and contrary to that suggested by Ozoga and Verme (1970) a sudden drop in ambient temperature cannot be accepted as an explanation for the lower urea-N recycled and lower N retention in wapiti in December, compared to that in October. Both IN and OUT wapiti showed parallel changes in urea-N recycled and N retention from October to April.

Hove and Jacobson (1975) reported that reindeer on a high protein

intake (68 g/d), cleared urea at an average rate of 21.6 l/d, whereas, reindeer on a low protein intake (24 g/d) cleared urea at an average rate of 1.8 l/d, suggesting that the reindeer on low protein intake were recycling more urea. Cocimano and Leng (1967) reported urea clearance rates of 0.92 to 4.29 $l/w^{.75}kg/d$ in sheep with N intakes of 0.240 to 2.52 $g/w^{.75}kg/d$, whereas wapiti cleared slightly less than one-half the urea-N as sheep on high N intake. Unlike the adult sheep, the wapiti were growing and therefore more N may have been retained for that purpose. Nonetheless, it was also noted that the growing wapiti had a high N retention for maintenance, which may reflect a lower urea-N clearance rate. Robbins et al. (1974) demonstrated that white-tailed deer fed low protein diets recycled a larger percentage of non-protein N than deer fed high protein diets, which may suggest that animals receiving low protein diets are able to reduce urea excretion as a result of increasing the solvent drag of urea from the late distal tubule and from the cortical and medullary collecting ducts (Knepper et al., 1976). Schmidt-Nielsen (1958) proposed among others (Lassiter et al., 1966; Clapp, 1966; Goldberg et al., 1967) that active absorption may also occur at the tubular level in animals on a low-protein diet. However, this mechanism is still questioned (Knepper et al., 1976) and if active reabsorption does occur, it is on a very insignificant scale (Mudge et al., 1973).

In this study, the wapiti in December and February had a lower N intake than in October, but clearance rate was relatively unchanged. This evidence suggested that the wapiti may have had a lower N retention during this same period. This was found to be the case. In addition, the negative correlation ($P<0.01$) of PUN to urea-N recycled

may suggest that some regulation by PUN for recycling urea-N may exist, as suggested by Thornton and Wilson (1972). The relationship of PUN with urea-N recycled is consistent with that reported in deer (Robbins et al., 1974) and in sheep (Cocimano and Leng, 1967).

High N retention and high N recycling may also be related to a high activity of fermentation in the rumen and hind gut. It was thought that the fermentative activity in the rumen regulated the proportion of urea-N excreted via the renal and digestive tract pathways, but Thornton and Wilson (1972) suggested from their study in sheep that urea excretion was regulated more by PUN. Fermentation activity has been shown to be affected by reticulo-rumen activity and dilution rate (Kennedy et al., 1977).

Changes in digestive and absorptive efficiencies may also occur. Harrop and Phillipson (1971) demonstrated that intravenously infused pentagastrin increased both urea entry into the rumen and urinary urea excretion in sheep. Very little work has been done on the relationships of urea-N recycling and hormone status in ruminants. This relationship may be an important concept for understanding the increased utilization of urea-N, protein and energy in northern cervids in summer compared to that in winter. The suggested increase in summer utilization of feed in wapiti may be very similar to the increased rates of protein deposition after realimentation observed in sheep and cattle following periods of prolonged feed restriction (Eckles and Swett, 1918; Wilson and Osborn, 1960; Keenan and McManus, 1969; McManus et al., 1972). However, more work is necessary for understanding how hormones may alter digestive efficiency.

The relationship between water intake and PUN in wapiti was not as strong as that observed in sheep by Kirk and Walker (1976a).

Kirk and Walker (1976a) reported a strong negative relationship of water intake with PUN. The relationship of urea-N excretion and water intake in the wapiti was similar to that reported in red deer and sheep (Maloiy *et al.*, 1970). Water intake and differential urinary loss of water and urea-N in the urine may be controlled by the antiduretic hormone (ADH). This hormone may promote both water conservation and urea concentration in the deep medullary regions of the kidney for recycling urea-N back to the digestive system (Mudge *et al.*, 1970; Schmidt-Nielsen and Pfeiffer, 1970), when animals experience low protein and/or water intakes. It has been observed that sheep (Schmidt-Nielsen and Robinson, 1970), camels (Schmidt-Nielsen and Osaki, 1958) and llamas (Engelhardt and Engelhardt, 1976) have the most effective urea conservation mechanism when fed low dietary levels of protein, compared to rats and dogs. The dynamics of ADH in reference to N recycling in wapiti during different seasons of the year may be an important mechanism during times of fattening, growth and starvation; and is, therefore, worthy of further study.

CHAPTER 9

SYNTHESIS: METABOLIC ADAPTATIONS

1.0.0. SEASONAL EFFECTS

The seasonal effects on digestion and nitrogen utilization observed in the wapiti may have been due to 1) the result of genetic programming driven by an entrainment agent (Zeitgeber) in this case being photoperiod, 2) the result of age of the wapiti and/or 3) an artifact of experimental procedure and design. The experimental results together with the results and conclusions in the literature strongly suggest 1) above.

Change in daylength is a powerful Zeitgeber that drives the biological circannual oscillator(s) of many migratory birds and fur bearing animals in the northern hemisphere. There has been indirect evidence that ruminants native to northern regions may also possess circannual oscillators sensitive to changes in photoperiod. This has been observed in cervids in their seasonal changes of hair coat (Ryder, 1977), antler and reproductive activity (Wislocki _et al_., 1947; Goss, 1977). The results of this study suggested that growing wapiti may have seasonal (photoperiod and age) changes in digestive efficiency. Growing wapiti may have a greater potential for growth during the summer than during the winter photoperiod. The mechanism for storing energy and protein by wild ruminants in winter and early spring may not be as important as in late summer and early autumn when both protein and energy are plentiful. This idea may be further supported by the work of Thorne

and Butler (1976). In August, 1973, male yearling wapiti had a 40.6% greater intake per kg$^{.75}$ than a mature cow offered the same pelleted ration in April-May, 1974. Similar results were obtained when hay was offered (36%). Differences due to age and sex may have accounted for some of the seasonal variation, however, it is doubtful that age and sex accounted for the entire difference. Although the yearling bulls consumed greater quantities of DM than the cows, the digestibility of DM for the yearling bulls was 18% and 13% higher than that for the mature cows for baled and pelleted hay, respectively. This is contrary to what is normally expected, i.e. as DM intake increases digestibility normally decreases. Similar and greater differences in the digestibilities of crude protein, crude fat, crude fiber and nitrogen free extract were reported, suggesting possible seasonal effects.

In addition, cervids reportedly have increased basal metabolic rate during summer and early autumn (Silver _et al._, 1969) and this may be associated with the increased potential for storage of energy and protein, compared to that in winter. Photoperiod may still serve as an important Zeitgeber for regulating the times of storage and the times of conservation of energy and protein in animals. This mechanism has been shown to occur in migratory birds. Meier and Burns (1976) were able to demonstrate in white-throated sparrows (_Fundus grandis_) that when prolactin injections were given late in the day fattening would occur; when prolactin injections were given early in the day, a loss of fat would occur. They were also able to show that daily adrenal corticosteroid injections given to birds exposed to constant lighting, resulted in the entrainment of daily rhythms of fattening in response to prolactin. This work was supported by the findings that corticosteroids

could directly set the daily rhythms of sensitivity to prolactin at the tissue level in the cropsacs of pigeons (John et al., 1972). In addition, they found the thyroid hormones to serve a permissive role in maintaining the corticosteroid rhythms.

In other male animals such as rabbits (Grigsby, 1976) and cattle (Lund-Larsen, et al., 1977) tropic hormones such as estrogen, testosterone and growth hormone have been shown to be most active during the summer and autumn compared to other times of year. It has been shown that testosterone is greatly reduced during the winter season in roe deer (Gimenz et al., 1975), reindeer and caribou (Whitehead and McEwan, 1973) and white-tailed deer (Bubenik et al., 1975). West and Nordan (1976) reported that somatotrophs in the pituitary appeared to be most active in spring and summer and lactotrophs most active in autumn whereas during the winter all the cells of the anterior pituitary showed the least signs of activity. Other workers (Enochs and Johnson, 1977) have demonstrated digestive hormones such as gastrin and pentagastrin to be important trophic hormones of the gut which are regulated by such hormones as thyroxine and growth hormone. Quay (1970) and Kappers (1971) who studied the relationships of the pineal gland and daylength in rodents have found that the pineal was sensitive to daylength and regulated many of the reproductive and metabolic hormone activities. These investigations and the results of this study indicate that daylength may be an important cue for regulating the hormonal status and hence metabolic activity of ungulates.

The advantages for the circannual rhythm of digestion and urea-N recycling in wapiti may be related to the circannual changes in plant phenology. During the summer months protein is not a limiting nutrient,

as it is during winter, and therefore, it is paramount that the wapiti can fully utilize its availability. Furthermore, as has been shown in this study in October, digestible protein may be further utilized with an increased capacity of recycling urea-N. Although the experiments were not carried over into the summer months, the trials in October and late spring suggested that the wapiti may have an increased recycling of urea-N and a higher digestible intakes during summer and early autumn, in preparation for winter when less feed is available and of poorer quality.

The implications of this study suggest that feed requirements of wapiti cannot be based on body weight and plant quality alone. If a given feedstuff is tested for its digestible content and its consumption during the winter months, the estimated utilization may be underestimated if the same feed were offered during the summer and early autumn periods. Therefore, not only is digestible intake shifted upward from winter to summer as a result of the quality of available feed, but also as a result of a greater physiological requirement of the animal itself. As this study indicated, N retention was greater during October and June than it was during December, February and April, and was partially due to a greater recycling of urea-N during October and June. Therefore in studying the utilization of feedstuffs by wild ruminants for purposes of supplementing their available feed on the range, it is recommended that trials be done for a given feed in both summer and winter for obtaining unbiased observations as a result of the probable effects of season on digestion and utilization of feedstuffs. Estimating range utilization and nutrient requirements of wapiti, digestible intake must be adjusted for season as a result of changes in digestion. Controlled

photoperiod experiments to determine the effect of photoperiod on digestion and urea-N recycling to the digestive tract in cervids, however, still requires further clarification and study.

The effect of age on digestion and urea-N recycled to the digestive tract, could not be partitioned in this study However, it has been reported (Church, 1973) that the ruminant stomach in sheep and goats reaches maturity in about 8 weeks, in deer about 3 to 4 months and in cattle about 5 to 6 months. In addition, it would be expected that digestive efficiency in a maturing stomach of a ruminant would increase with time rather than decrease, since the stomach wall thickness and its associated villi progressively become mature for absorption of nutrients. In the wapiti, digestible intake of feedstuffs and the retention of N were high in October and then decreased thereafter until June, when the IN wapiti were observed to increase digestible intake. The IN wapiti showed signs of being approximately one to two months ahead of the OUT wapiti in summer photoperiod. This observation appeared to indicate that age may have contributed very little variation to the effects of season.

As to the seasonal effects being an artifact of experimental procedure, the analysis of variance indicated insignificant variation between animals, as well as all the interactions between major variables accounted for in the error term. All parameters investigated compared favorably with those reported in the literature.

Thus it is concluded that changes in digestible intake and urea-N recycled to the digestive tract is less active during the winter season than during the summer season and may be largely the result of changes in photoperiod.

2.0.0. TEMPERATURE EFFECTS

The effect of temperature on digestibility and urea-N recycled to the digestive tract may have been due to changes in temperature *per se*, humidity and barometric pressure. However, the effect of temperature *per se* and humidity could not be partitioned in the experimental design and, therefore, were considered as one parameter. The effects of barometric pressure are related to changes in weather patterns and were assumed to affect both IN and OUT wapiti equally.

DM intake of both temperature treatments were similar and contributed very little, or no variation to the differences of digestibility of E and ADF in the wapiti. The thyroid hormones also appeared to contribute very little to the digestive differences between temperature treatments contrary to that suggested by Westra (1975) and Kennedy *et al.* (1977). It is possible that the cold temperatures in December activated both intra-abdominal and spinal thermoreceptors (see discussion of Westra, 1975) which caused increased gut motility and therefore decreased MRT. This is still not clearly understood. This study also suggested that less digestible components may be passed out of the digestive tract quickly and the more digestible components retained and absorbed (Johnson, 1976). This digestive characteristic may be very advantageous on winter rangelands when cell wall constituents (CWC) in forages are high compared to spring and summer. It has been shown in vitro that when CWC increase, digestibility decreases (Short *et al.*, 1974).

Contrary to what was expected, recycling of urea-N to the digestive tract was very little affected by temperature treatment. Recycling of urea-N was increased only when feed intake was insufficient to maintain N balance in early spring (April), or in mid-autumn and late spring when

protein and fat were being actively deposited in body stores. Voluntary reduction of feed and water from winter to summer may be an advantage to the animal when feed is both less available as a result of increasing snow depths, and of lesser quality. It has been reported that active feeding activity may be terminated completely in severe weather when behavioral means of conserving energy is more important as a means to possessing a balanced energy budget. For instance, it was observed in both deer (Holter et al., 1975) and cattle (Clark et al., 1972; Malechek and Smith, 1974) that less time was spent grazing and more time spent lying down or standing idle in low sheltered land depressions during very cold and windy weather, than during warm weather conditions. This activity was difficult to assess in the wapiti, yet during windy cold days, the wapiti were noticed lying down more and appeared to be more reluctant to being moved than usual. It is well documented that a lying posture not only reduces heat loss from the extremities, but reduces energy expenditure due to activity in search of feed. It also permits a thicker insulative layer of still air to surround the animal body for increased protection in losing body heat.

The implications of this delicate energy and protein balance maintained by wapiti during winter and early spring may attest to the importance of suitable shelter as well as sufficient browse during times of cold and deep snow conditions. Harassment by predators and human activity also could mean large energy deficits leading to a rapid and dangerous depletion of energy reserves during times of severe cold. Recycling of urea-N may then be a important mechanism to retain N when intake of N is less than adequate for maintenance. In contrast to winter, the summer period should provide an adequate high quality

forage for building body reserves quickly, and sufficiently for winter readiness.

3.0.0. PRELIMINARY MODEL

The flow-model, illustrated in Figure 16, is a suggested summary of the effects of season and temperature on the rate and flow of the various parameters of metabolic activity in a growing wapiti.

Based on the data of this study, in summer to mid-autumn wapiti may have a 20 to 30% greater DM intake, relative to that in winter. DM, E and N digestibility may be 2 to 4% lower in summer, than in winter, but in winter when fiber content is much less digestible, feed may be passed out of the digestive system much faster (lower retention time of feed particles). Thyroid hormone concentrations in the serum were observed to increase in November and December when retention time was observed to decrease. During times of low temperatures in winter, the digestibility of ADF and E were reduced. Retention time of digesta in wapiti also increased when temperatures were low, relative to that when temperatures were mild. Thus, as shown in Figure 16, both season and temperature influenced digestibility and maintenance energy, whereas, only season influenced DM intake.

During winter, basal metabolic rate was shown by other workers to be lower; therefore, growth rate and plane of nutrition tended to be lower than that determined in summer. Total work activity in winter was expected to be greater than that in summer because of the decreased availability of food and the increased work in travelling in snow.

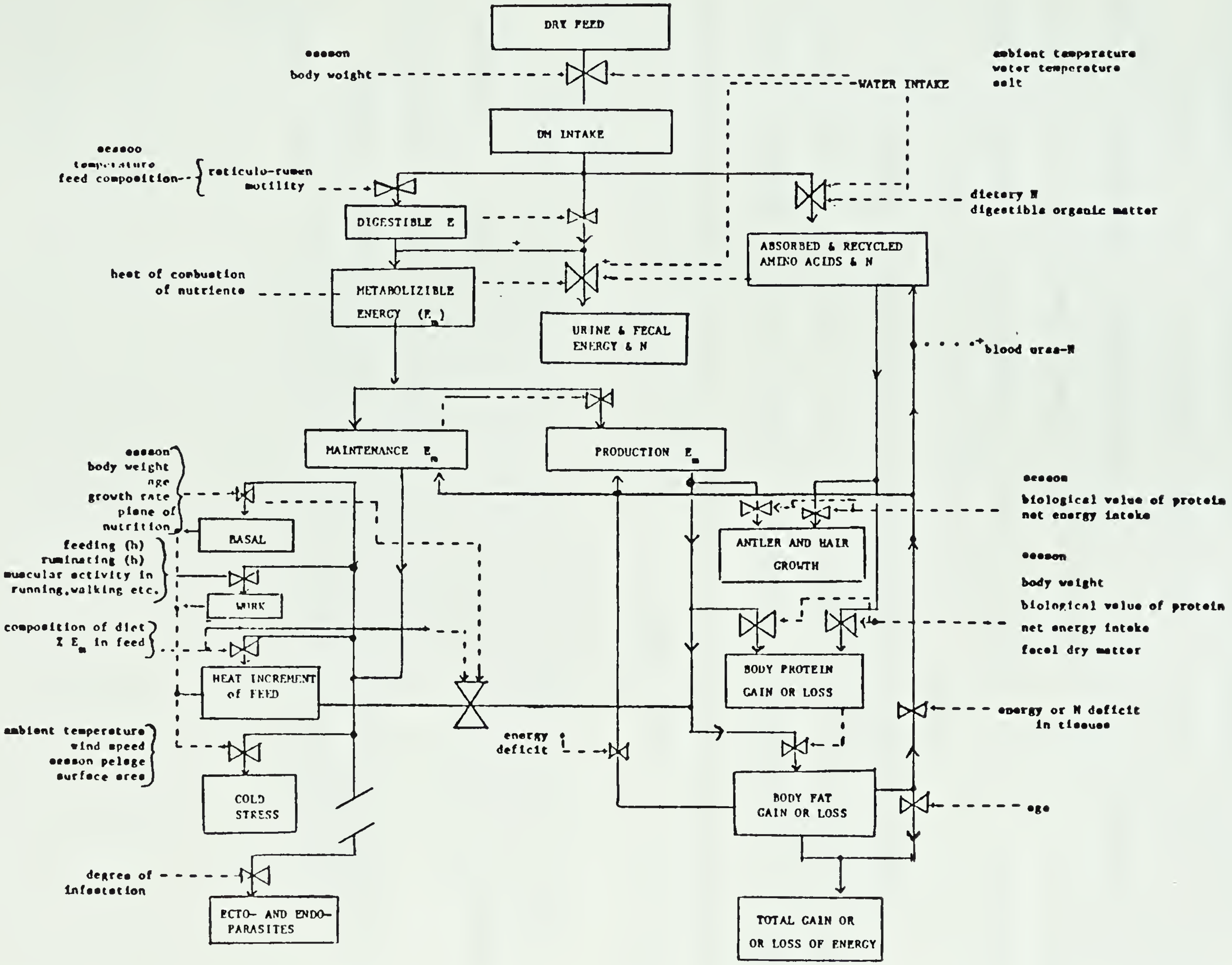

Figure 16. Flow--diagram model describing the effects of temperature and season on metabolism in wapiti. Adapted from the model described by Graham *et al.*, 1976.

However, overall activity may be reduced compared to summer in an attempt to balance the E and N budgets. Pelage condition, body size and body reserves were also discussed as important means for the wapiti to withstand cold stress and for its ultimate survival in winter.

On the N side of the balance, photoperiod has been shown to regulate antler development and hair growth. In autumn and mid-spring, the pelage of the wapiti was renewed, and in January antlers began growing. Urea-N recycled to the digestive tract was shown to be seasonally regulated, being most active during October, thereafter urea-N recycled to the digestive tract dropped to lower levels. When N intake was insufficient to maintain N balance in April, urea-N recycled increased in what appeared to be an attempt to prevent a large deficit. Nitrogen retention was also about 30 to 90% greater in October than in December to April, whereas in June, N retention increased from 20 to 50% from that in April.

Temperature had little or no effect on N metabolism in wapiti. It appeared that during the winter the N recycled was indirectly related to N intake when there was a N maintenance deficit.

PUN was found to be a poor indicator of nutritional status in wapiti, since it was related to water intake, season and possibly age.

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APPENDICES

APPENDIX 1. Metabolic crates used in wapiti study.

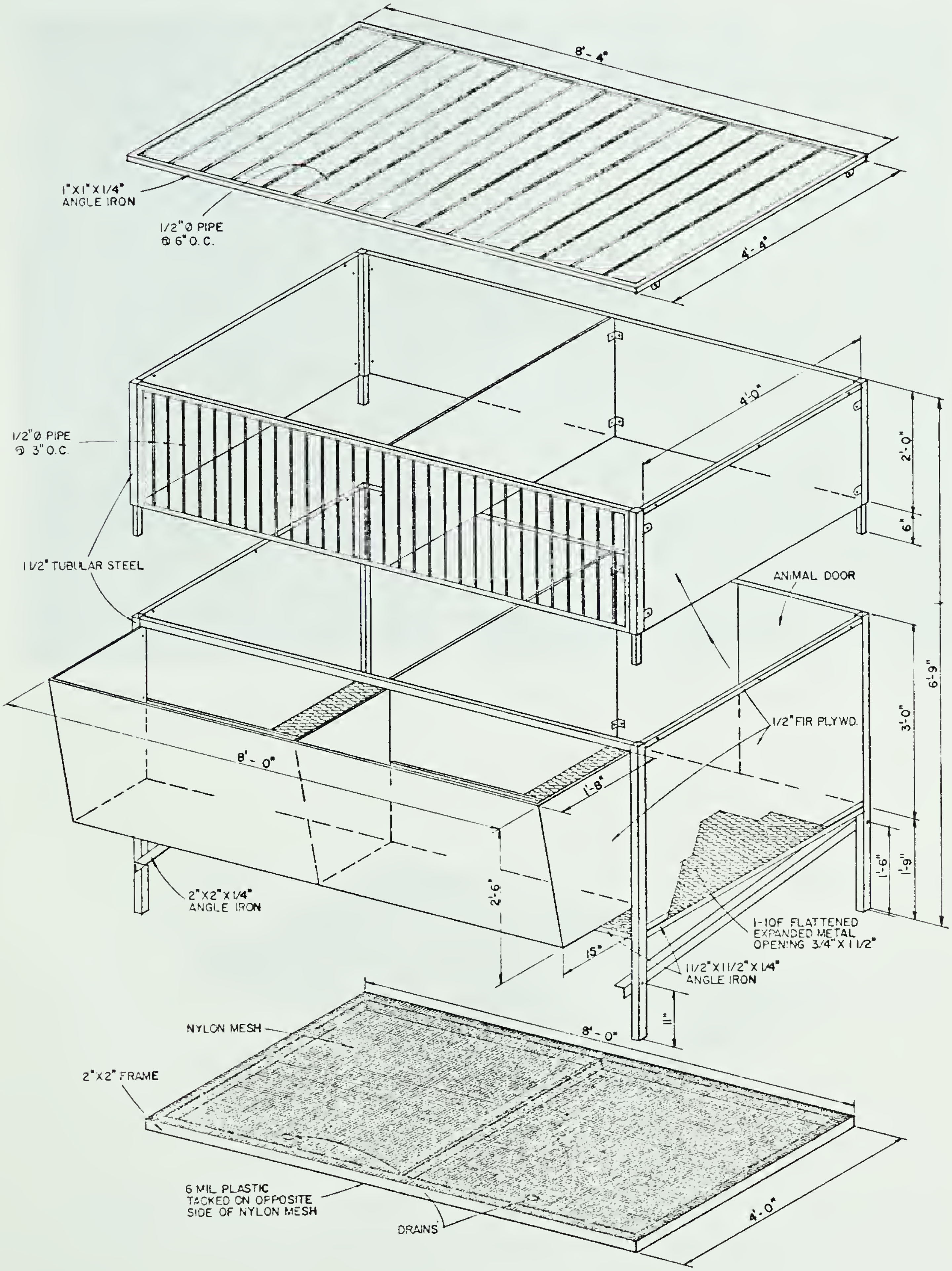


Figure 1. Metabolic crate initially designed for deer.

APPENDIX 1. Metabolic crates used in wapiti study.

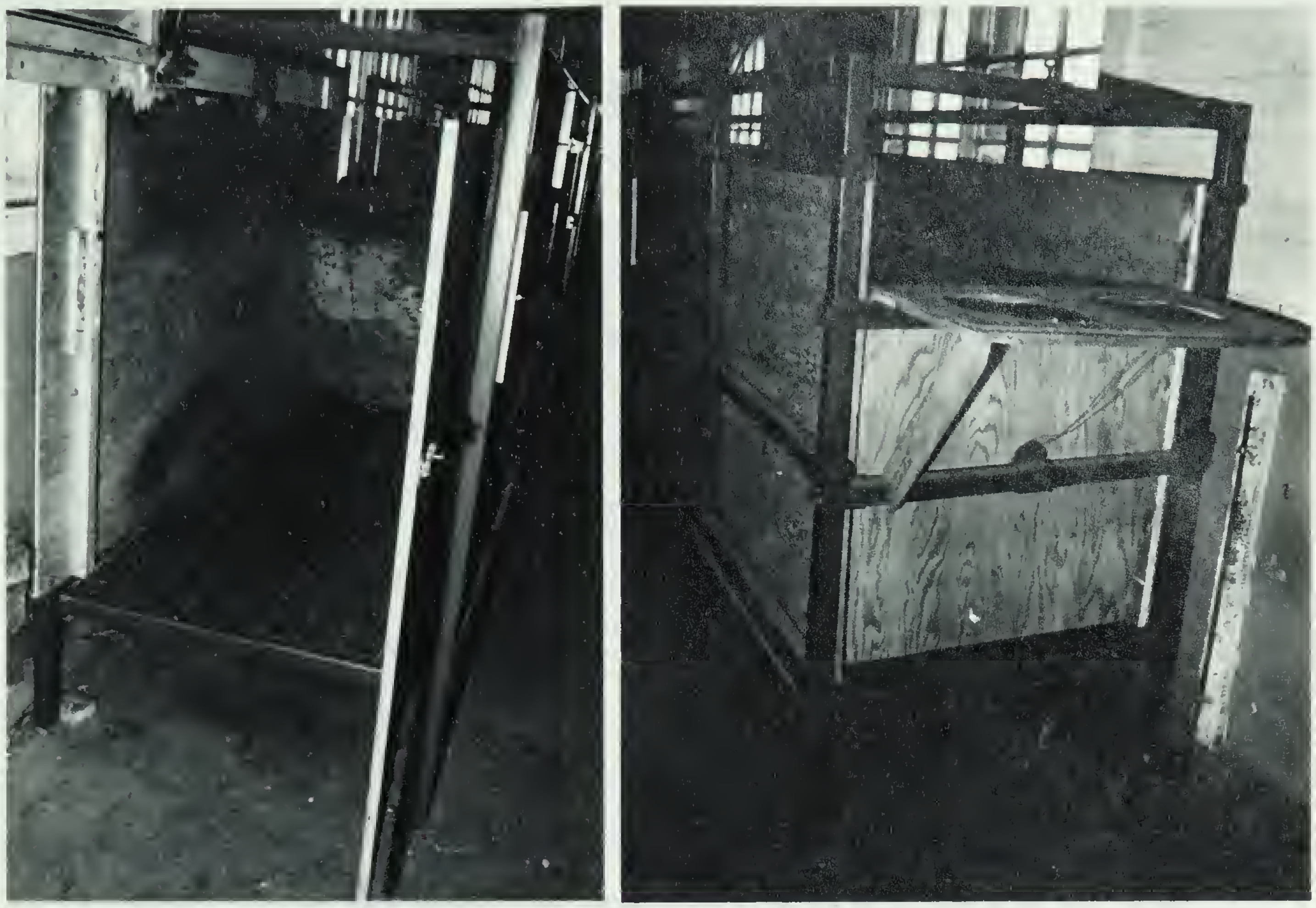


Plate 1. Large cattle metabolic crates modified to hold one wapiti.

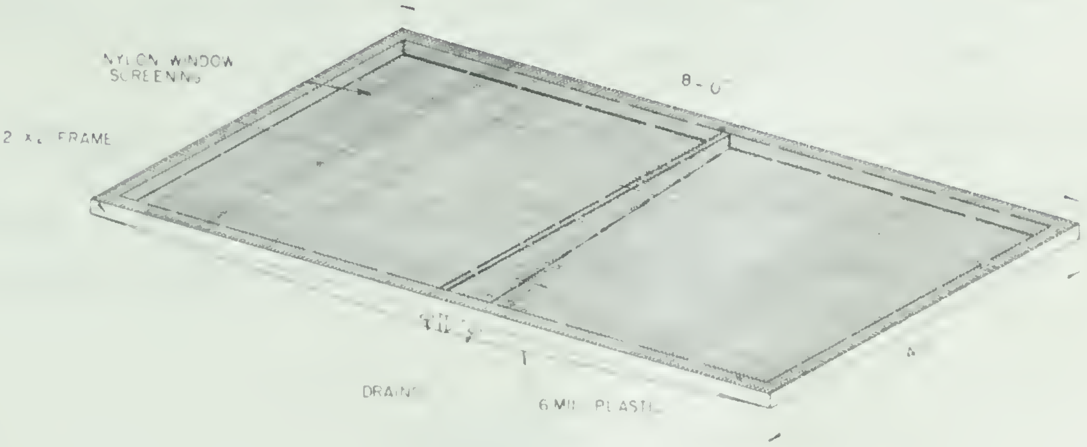


Figure 2. The fecal and urine collection apparatus constructed to fit the large cattle metabolic crate shown above.

APPENDIX 2

Model A

$$Y_{ijk\ell m} = \mu + E_i + T_j + ET_{ij} + U_{k(j)} + EU_{ik(j)} + A_{\ell(jk)} + \varepsilon_{m(ijk\ell)}$$

where: $Y_{ijk\ell m}$ = the $ijk\ell m$th observation.

μ = the population mean

E_i = the effect of the i^{th} experiment ($i = 1, 2 \ldots 5$).

T_j = the effect of the j^{th} temperature treatment ($j = 1,2$).

ET_{ij} = the effect of the i^{th} experiment and the j^{th} temperature treatment.

$U_{k(j)}$ = the effect of k^{th} unit nested in the j^{th} temperature treatment.

$EU_{ik(j)}$ = the effect of the i^{th} experiment and the k^{th} unit nested in the j^{th} temperature treatment with 2 degrees of freedom lost as a result of 2 wapiti within one unit missing in the last 2 experiments.

$A_{\ell(jk)}$ = the effect of the ℓ^{th} wapiti nested within the k^{th} unit nested in the j^{th} temperature treatment.

$\varepsilon_{m(ijk\ell)}$ = the residual random term m, with a variance of τ^2.

Two degrees of freedom were subtracted from the EU interaction because wapiti 1135 and 1139 were missing in two animal cells.

Model B

$$Y_{ijokn\ell m} = \mu + E + T_j + C_o + U_{k(j)} + W_{n(i)} + TW_{jn(i)} + CE_{oi} + ET_{ij} + CT_{oj} + EU_{ik(j)} + A_{\ell(jk)} + \varepsilon_{m(ijokn\ell)}$$

APPENDIX 2

Model B continued...

where: $Y_{ijokn\ell m}$ = the $_{ijokn\ell m}$ observation.

μ= the population mean.

E_i = the effect of the i^{th} experiment (i=1,2...5).

T_j = the effect of the j^{th} temperature treatment (j=1,2).

C_o = the effect of the o^{th} crate/pen (0=1,2).

$U_{k(j)}$ = the effect of the k^{th} unit nested in the j^{th} temperature treatment.

$W_{n(i)}$ = the effect of the n^{th} week nested in the i^{th} experiment.

$TW_{jn(i)}$ = the effect of the j^{th} temperature treatment and the n^{th} week nested in the i^{th} experiment.

CE_{oi} = the effect of the o^{th} crate/pen and the i^{th} experiment.

ET_{ij} = the effect of the i^{th} experiment and the j^{th} temperature treatment.

CT_{oj} = the effect of the o^{th} crate and the j^{th} temperature treatment.

$EU_{ik(j)}$ = the effect of the i^{th} experiment and the k^{th} unit nested in the j^{th} temperature treatment with 2 degrees of freedom lost as a result of 2 wapiti within one unit missing in week 2 of experiment 3, and experiments 4 and 5.

$A_{\ell(jk)}$ = the effect of the ℓ^{th} wapiti nested in the k^{th} unit nested in the j^{th} temperature treatment.

$\varepsilon_{m(ijokn\ell)}$ = the residual random term m, with a variance of τ^2.

APPENDIX 3A. Antler anomalties.

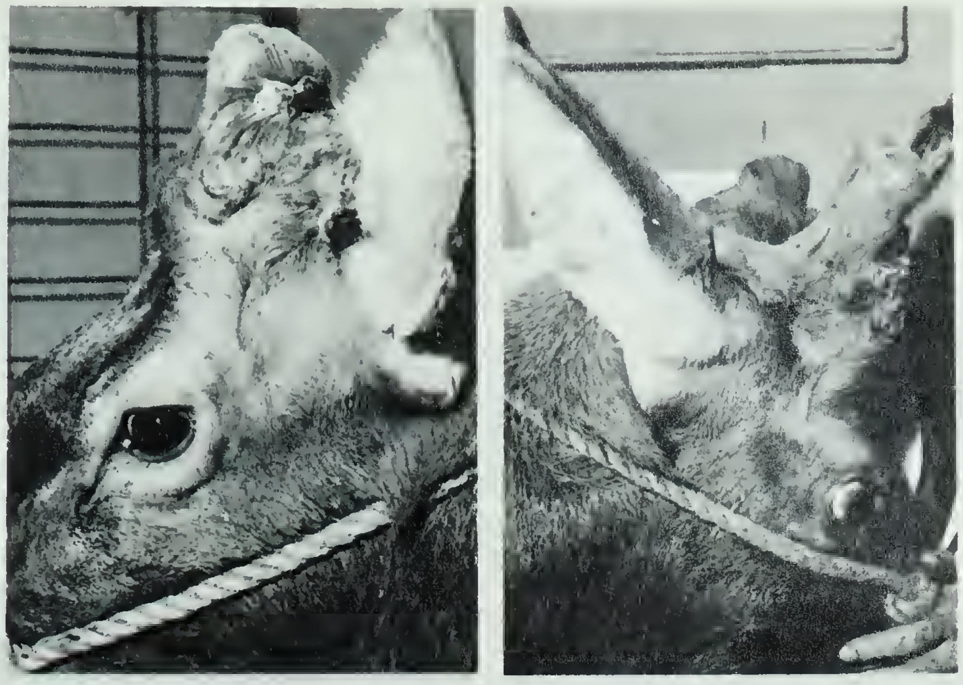


Plate 1. Antler regrowth with the previous antler still retained. Wapiti 1137 on June 3, 1977.

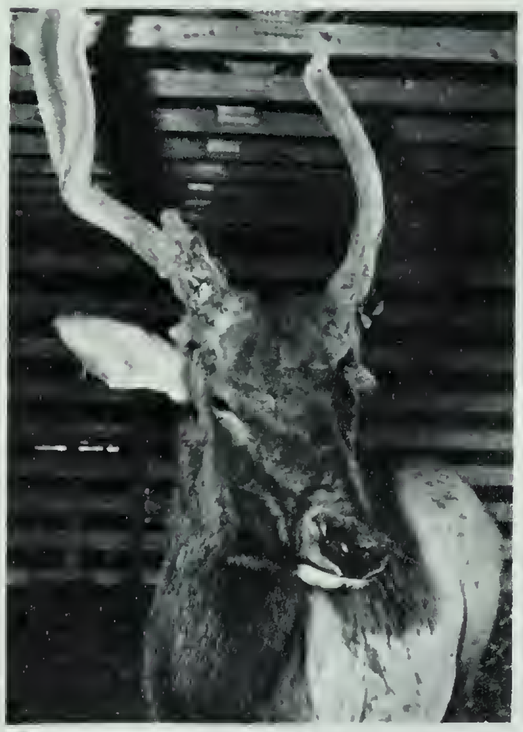


Plate 2. Growth of second set of antlers by mid-July, 1977 by wapiti 1137.

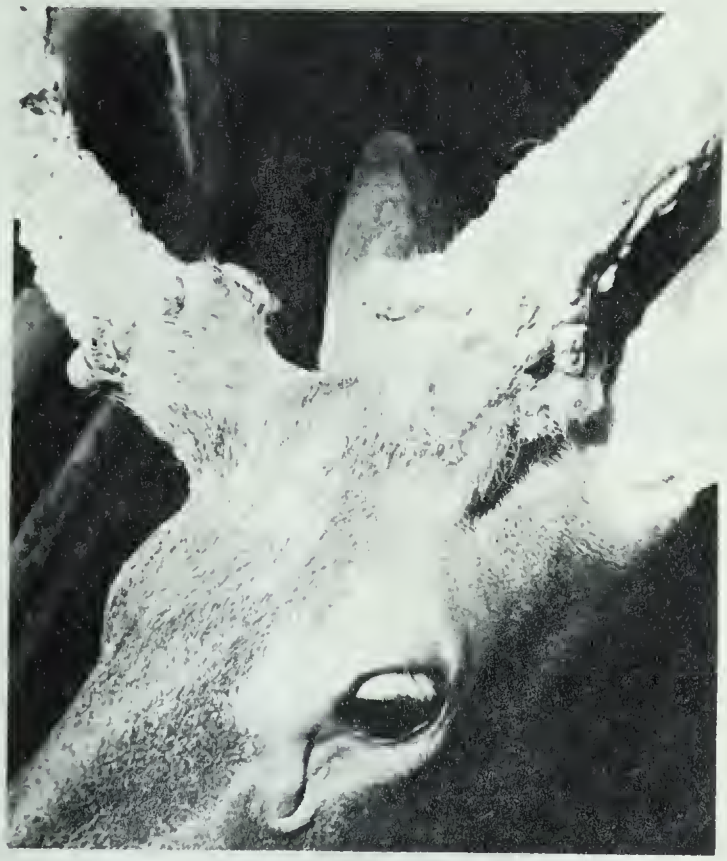


Plate 3. Antler protruberances of wapiti 1133.

APPENDIX 3B. Individual photographs of wapiti March 1, 1977.
(wapiti 1134, March 21, 1977)

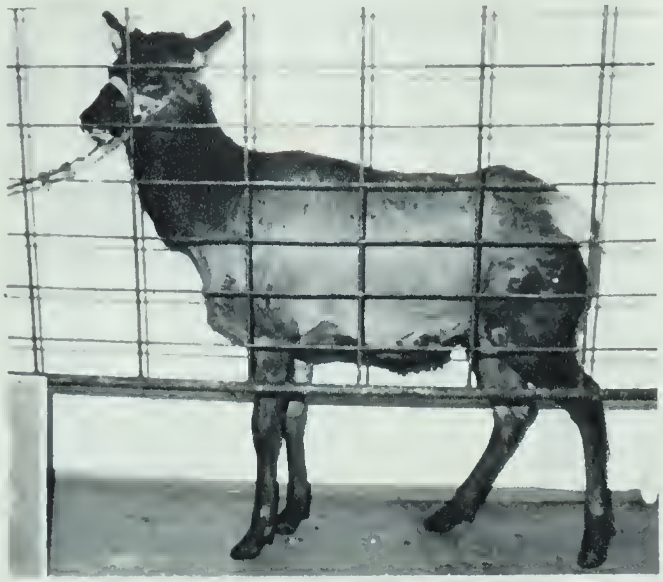


Plate 1. OUT wapiti 1128.

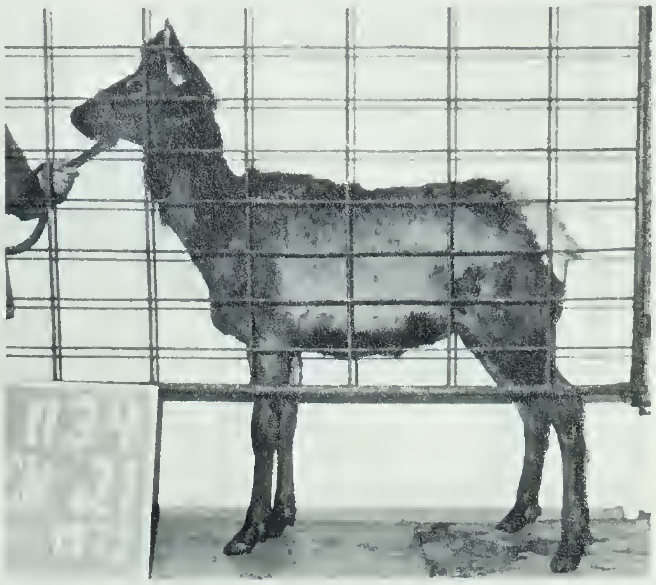


Plate 2. OUT wapiti 1134.

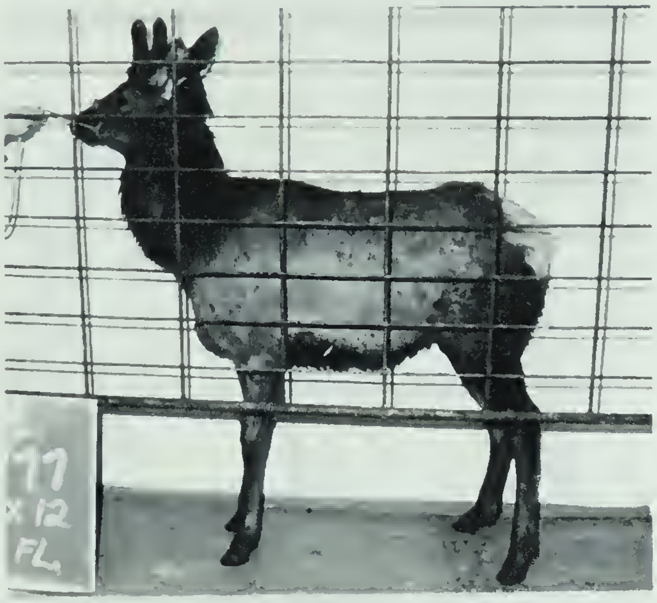


Plate 3. OUT wapiti 1136.

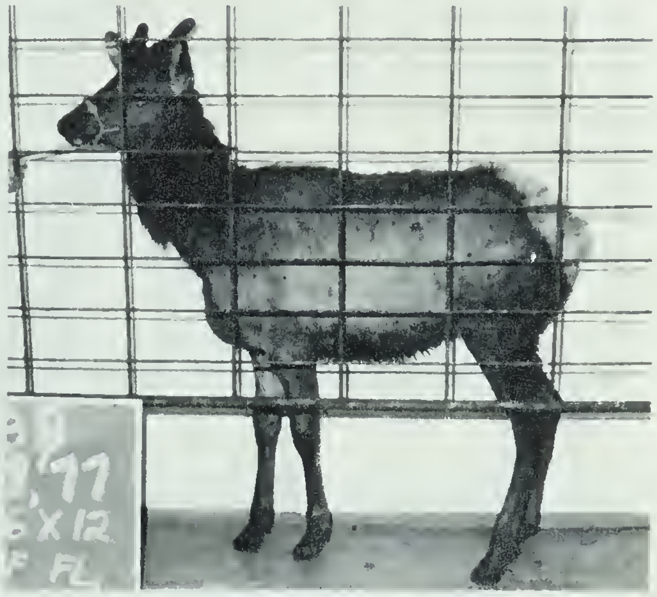


Plate 4. OUT wapiti 1138

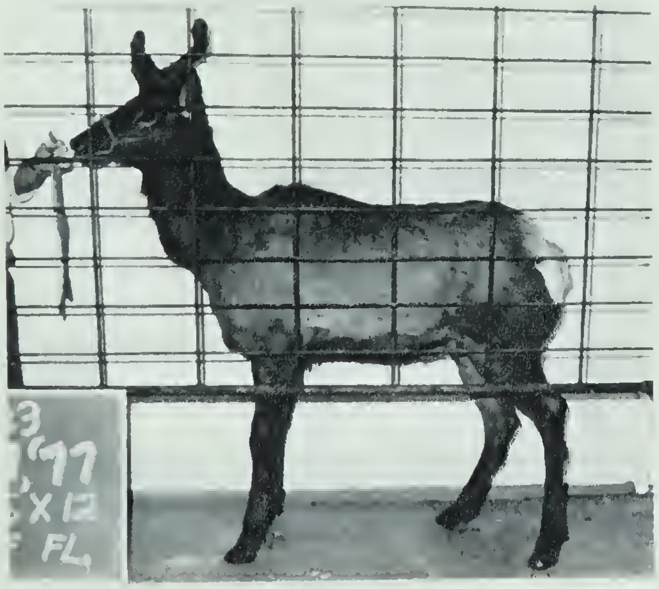


Plate 5. IN wapiti 1133.

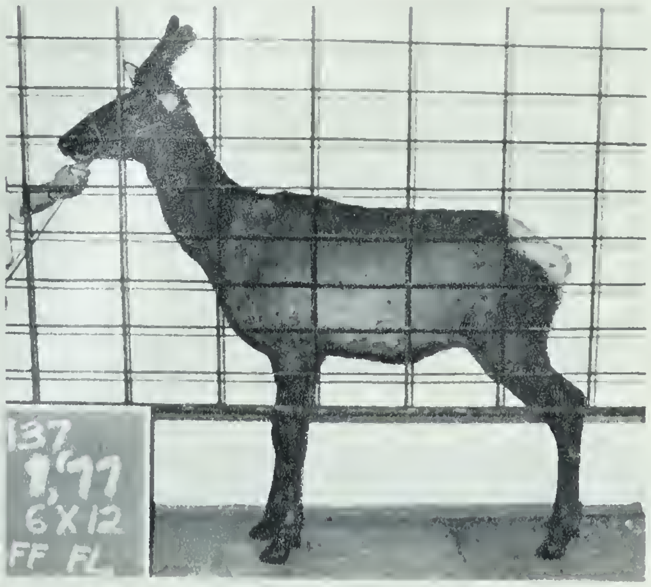


Plate 6. IN wapiti 1137.

APPENDIX 3C.   Individual photographs of wapiti June 16, 1977.

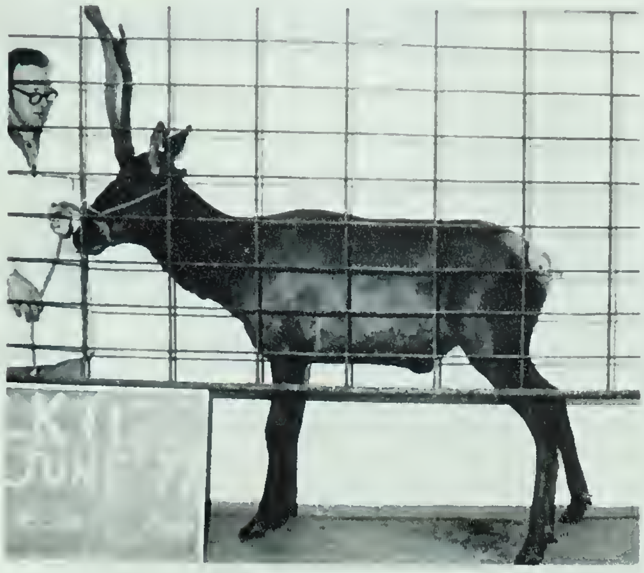
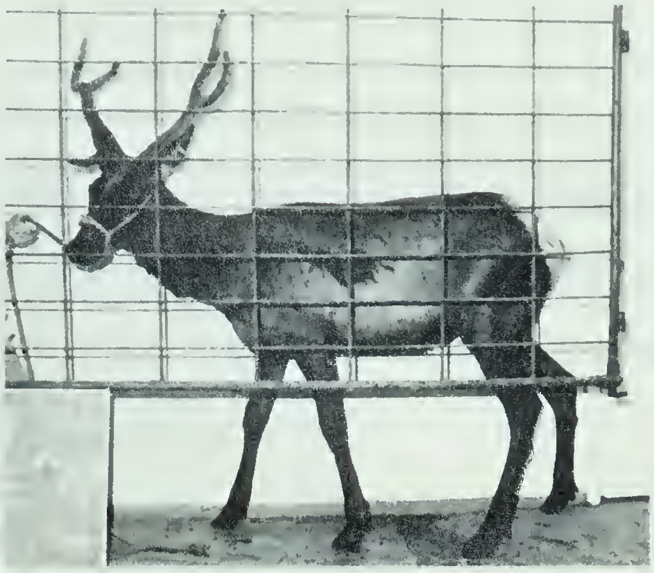


Plate 1. OUT wapiti 1128.



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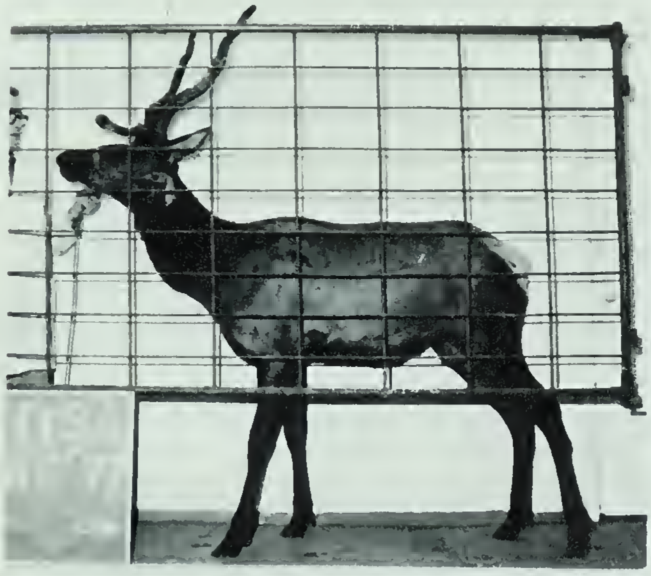

Plate 3. OUT wapiti 1136.

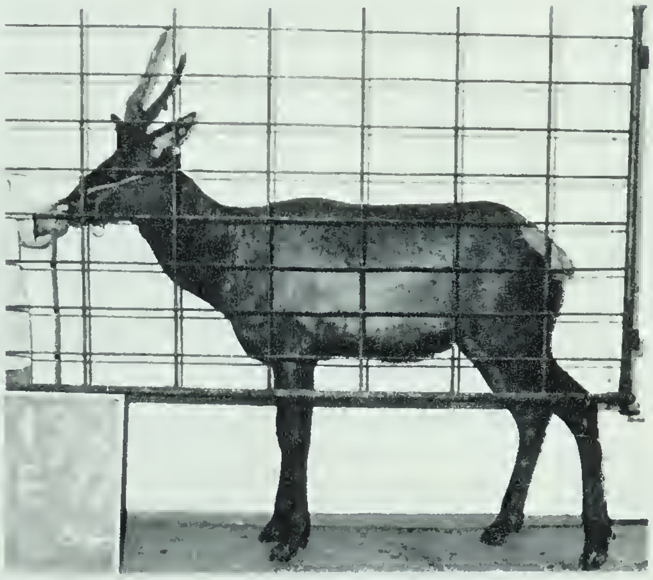

Plate 4. OUT wapiti 1138.

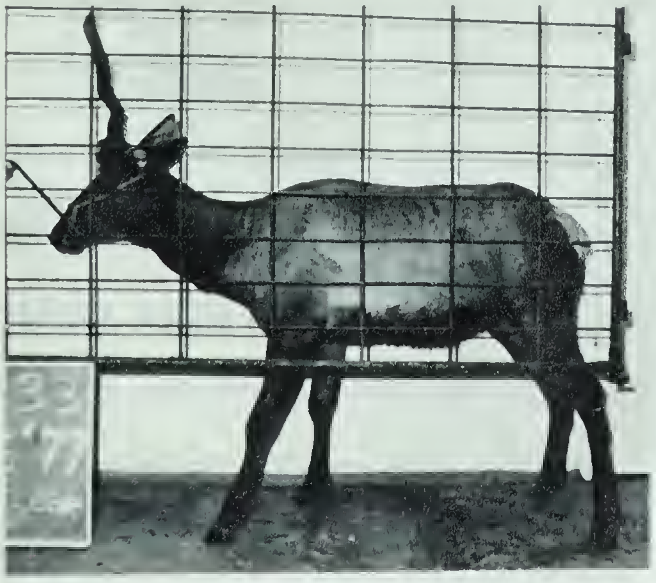

Plate 5. IN wapiti 1133.

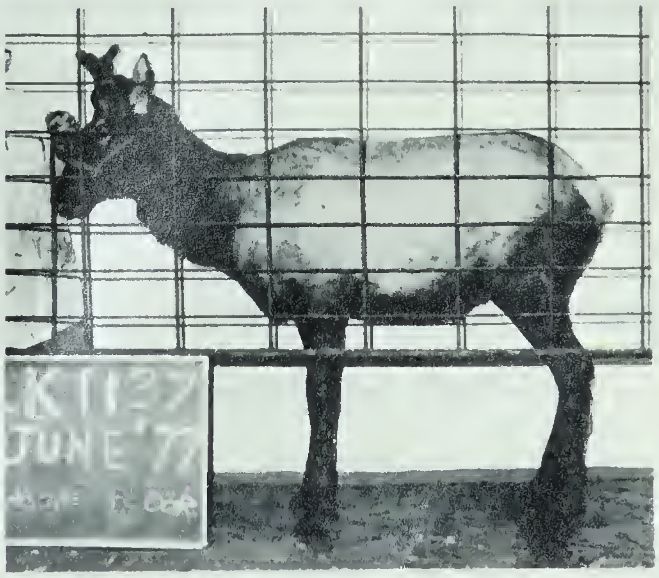

Plate 6. IN wapiti 1137.

APPENDIX 4

MILK DIGESTION EXPERIMENT

An experiment was designed to compare the apparent digestibility of several nutritive components and the mean retention time (MRT) of digesta in wapiti calves fed two separate milk rations. The experiment was conducted between July 3 and July 7, 1976.

METHODS AND MATERIALS

To determine the apparent digestibility and rate of passage of the two milk rations used in the calf rearing program, eight male and two female wapiti calves were divided into two equal groups, one group receiving a ration consisting of a mixture of 15 oz. of *Alpha* evaporated milk and one liter of *Palm* homogenized milk (milk), and the other group receiving lamb milk replacer (*Supertreat*). The *Supertreat* ration (Table 1) was diluted 1:4 with warm tap water. The two rations were offered at 900, 1200, 1600 and 2000 h daily in one liter soft drink bottles fitted with lamb nipples. They were cooled to about 5 C before being offered to the calves. Each calf was offered the volume of ration it was consuming the week before the experiment (Table 1, Appendix 4). The calves were allowed to adjust to their rations one week before the experimental trial began. Daily samples of each ration were frozen for later analysis. Water was available *ad libitum*.

Calves were kept in individual pens 8 x 4 ft. on concrete floors in a barn held at a constant temperature (20C). Photoperiod was by natural lighting.

Total fecal collections were made by palpating the perineum with a damp paper towel in one hand and collecting the feces in a plastic bag with the other. Fecal collections were made in this manner every 3 hours after a single oral dose of ^{103}Ru [^{103}Ru-labelled tris (1,10-phenanthroline) ruthenium (II) chloride] was given. The ^{103}Ru label was prepared as described by Tan et al.(1971). Two more fecal collections were made after the last collection within which no radiation could be dectected using a survey meter (Model 2650, Nuclear-Chicago Corp.).

Each fecal sample was air-dried at 65 C and ground in a micro-mill grinder (Techmar, Model no. A10, Can-Lab Supplies) and weighed into Beckman Biogamma vials (Beckman Instruments, Fullerton, Calif.). The samples were then counted for 10 min. with a Beckman Biogamma Counting System (Beckman Instruments). Samples of the stock solution ^{103}Ru were counted using the same procedure.

Mean retention time (MRT) was calculated using the formula:

$$MRT = \sum_{i=1}^{n} t_i M_i$$

where: t_i is the time elapsed between dosing and the mid-point of the ith time interval and M is the fraction of the total amount of matter excreted in the ith time interval (Faichney, 1975).

Dry matter (DM), gross energy (E), nitrogen (N) and ether extract (fat) digestibility for each ration was calculated according to standard procedures.

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Table 1. The effect of two milk rations on digestion.

ELK ID	Ration	DM in ration %	DM Intake g/d	DM Intake g/w$^{.75}$kg/d	Digestibility Coefficients DM %	E %	N %	Fat %	MRT h	Time First Appearance ^{103}Ru(h)	% DM in feces	Wt. gain g/d	g DM intake per g of gain
1129	milk	16.7	295.5	31.1	95.2	96.2	91.4	99.3	28.7	12.5	28.9	170.4	1.72
1131	m "	"	279.8	30.3	94.5	95.5	91.0	99.3	48.3	18.5	34.7	113.6	2.45
1135	"	"	263.9	33.3	96.1	97.0	93.0	99.6	41.4	12.5	32.8	113.6	2.31
1138	"	"	350.9	29.8	91.8	92.	90.2	98.0	22.4	6.5	34.3	0	-
1139	"	"	309.0	31.1	87.2	90.8	86.4	98.9	32.4	15.5	39.7	0	-
Mean	"		299.8	31.1**	93.0	94.4	90.4*	99.0**	34.6	13.1	34.1	79.5	
S.D.				±1.3	±3.6	±2.2	±2.2	±0.6	±10.3	±4.4	±3.9		
1132	Super-	21.3	384.7	39.7	88.6	91.0	80.4	97.9	27.9	12.5	34.4	113.6	3.34
1133	treat	"	384.7	35.2	93.3	94.9	86.5	97.1	23.4	12.5	25.6	0	0
1134	"	"	384.7	38.7	93.7	95.0	86.2	97.7	30.7	12.5	28.2	227.3	1.67
1136	"	"	384.7	37.7	90.4	92.5	84.6	97.4	37.8	12.5	31.3	113.6	3.34
1137	"	"	460.8	36.7	90.8	92.7	84.1	96.9	46.0	12.5	28.4	113.6	4.06
Mean			399.9	37.6	91.4	93.2	84.4	97.4	33.2	12.5	29.6	113.6	
S.D.				±1.05	±2.1	±1.5	±2.2	±0.4	±8.9		±3.4		

** - Significantly different between treatments ($P<0.01$) Student's t-test
* - Significantly different between treatments ($P<0.02$) Student's t-test

S.D. - standard deviation; E - gross energy; N - nitrogen; Fat - ether extract;
MRT - mean retention time of ^{103}Ru.

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Table 2. Body weights (kg) of wapiti from birth (1976) to one year old (1977.

	Wapiti ID										
Date	1128	1129	1131	1132	1133	1134	1135	1136	1137	1138	1139
Birth	11.8	14.5	15.9	14.1	16.4	15.9	13.2	14.5			
Jun 8	11.4	13.2	13.2	14.5	16.8	15.0	12.0	14.5	20.0	19.8	17.0
18	14.3	16.6	16.0	16.8	19.3	17.2	13.2	18.2	23.2	23.6	18.9
27	15.9	18.7	18.1	18.5	20.8	18.6	14.1	20.0	26.1	25.2	18.6
Jul 5	17.5	20.2	19.3	20.4	23.2	20.9	15.7	22.0	29.1	26.6	21.4
15	22.3	25.0	23.6	24.5	26.8	23.9	20.0	25.9	33.2	30.7	23.6
26	26.6	27.5	26.1	29.1	32.5	28.6	23.0	30.7	39.5	32.7	26.4
Aug 5	31.3	31.6	29.9	33.6	36.4	32.6	27.5	35.5	44.0	36.4	27.5
16	35.7	33.2	34.8	39.3	40.0	33.6	30.2	41.1	50.0	41.4	25.5
25	36.1	35.7	42.0	44.5	45.9	40.5	33.9	46.8	54.1	45.7	27.7
Sep 8	47.3	38.6	50.9	54.3	52.7	50.2	37.7	53.0	65.7	52.5	32.3
Oct16	80.0				87.3	83.2	64.5	87.7	97.7	75.9	59.5
24	88.2				89.5	89.1	71.4	93.6	101.8	82.3	63.6
Nov 3	94.5				98.2	97.7	77.3	99.5	108.6	92.3	70.4
16	100.4				105.0	104.0	83.6	109.0	115.0	101.4	78.6
30	106.8				114.1	113.2	90.0	114.1	124.5	109.1	86.8
Dec10	107.3				114.5	118.2	93.2	116.8	128.6	111.4	90.0
19	111.4				121.8	122.3	94.1	119.5	134.5	114.1	94.5
29	112.8				127.3	128.6	99.1	124.1	131.8	119.5	100.4
Feb 4	130.4	102.7	133.6	140.9	141.8	144.5	117.3	140.9	154.1	143.6	124.1
12	129.5	109.1	138.2	144.1	144.1	140.0	114.1	139.0	155.0	145.0	119.5
23	132.3	110.0	145.0	149.5	148.2	148.2		147.7	161.4	150.9	
Mar21	144.5	121.4	148.2	155.4	165.0	165.9		158.2	198.2	166.8	
Apr11	147.7	126.8	153.2	159.5	165.9	163.2		167.7	198.6	178.6	
21	150.9	128.6	153.0	162.2	169.5	168.6		165.0	200.0	179.5	
May 5	150.9				178.6	177.3		166.8	203.6	182.7	
24	165.9				183.6	177.3		178.6	204.5	200.0	
Jun 3	173.2				188.6	179.5		174.1	210.0	198.2	
16	175.9				201.8	186.8		185.9	223.2	201.8	

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Table 3. Sex, location of birth, birth date, weight at birth and the derived theoretical von Bertalanffy coefficients of the wapiti used in this study.

Animal ID	Sex	Location of Birth	Birth Date	BW at birth (kg)	Theoretical von Bertalanffy coefficients			
					A	b	k	S.E.
1128	M	W	June 1	11.8	223	0.682	0.00546	4.72
1129	F	W	May 29	14.5	295	0.661	0.00316	1.17
1131	F	W	May 29	15.9	355	0.697	0.00345	3.47
1132	F	W	May 26	14.1	325	0.695	0.00394	2.93
1133	M	W	May 29	16.1	273	0.661	0.00480	3.77
1134	M	W	May 29	15.9	358	0.723	0.00344	3.08
1135	M	W	May 29	13.2	265	0.682	0.00499	5.29
1136	M	W	May 27	14.5	236	0.676	0.00570	4.25
1137	M	UF	May 28	-	331	0.649	0.00462	4.26
1138	M	UF	May 22	-	388	0.687	0.00342	4.18
1139	M	UF	May 25	-	700	0.719	0.00138	1.26
Overall average for males					313	0.686	0.00415	8.99
Overall average for males with 1139 deleted					290	0.680	0.00453	8.42
Overall average for females					331	0.686	0.00347	6.22

A - asymptotic body weight; b - scaling parameter; k - maturing index constant; S.E. - standard error of the mean.

M - male; F - female; W - Wyoming; UF - University Farm.

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Table 4. Effect of temperature on blood parameters.

Experiment	Temperature Treatment	PCV %	WBC mm^3	Lymphocytes %	Neutrophiles %	Plasma Calcium mg%	Plasma Inorganic Phosphate mg%	Plasma Creatinine mg%	Serum T_4 µg%	Serum T_3 ng%	Serum Alkaline Phosphatase U/L
1	OUTDOOR	39.1	4950	43.9	48.5	15.1	11.0	1.10	6.7	119.2	100.5^{bc}
	INDOOR	40.4	4650	44.1	51.9	14.3	12.1	1.12	5.8	127.2	131.5^{b}
2	OUTDOOR	42.6	8100	44.6	43.4	12.7	11.6	1.27	6.5	109.2	81.5^{c}
	INDOOR	37.9	7800	46.6	41.1	12.3	10.8	1.40	5.7	94.0	98.5^{bc}
3	OUTDOOR	36.6	5050	44.9	46.4	11.9	10.3	1.40	5.3	73.0	84.5^{c}
	INDOOR	33.6	6750	35.5	50.6	12.6	9.6	1.42	6.1	85.2	126.5^{b}
4	OUTDOOR	43.7	6650	61.2	33.4	12.4	10.1	1.40	4.7	81.5	114.5^{bc}
	INDOOR	45.5	7567	74.9	19.6	11.8	10.0	1.55	5.0	57.2	189.5^{a}
5	OUTDOOR	45.2	4800	63.8	21.3	12.0	10.3	1.67	3.8	62.5	96.5^{bc}
	INDOOR	49.0	5117	51.8	18.9	11.6	8.7	1.75	4.5	51.7	182.5^{a}
Average	OUTDOOR	41.5	5910	51.7	38.6	12.8	10.6	1.37	5.4	89.1	95.5*
	INDOOR	41.3	6377	50.6	36.4	12.5	10.2	1.45	5.4	83.1	145.7

abc - when letters differ (within columns) the values are significantly different ($P<0.01$). Duncan's New Multiple Range Test.

PCV - packed cell volume, WBC - white blood cells; T_4 - thyroxine; T_3 - triiodothyronine

* the temperature means are significantly different from zero ($P<0.001$).

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Table 5. The effect of season (experiment) and crate/pen effects on nutrient intakes and apparent digestibility.

Experiment	DM intake $g/w^{.75}kg/d$	P intake g/d	Ca intake g/d	Total Water Intake & feed $ml/w^{.82}kg/d$	Apparent Digestibility Coefficients					
					DM %	N %	Fat %	ADF %	NDF %	Hemi-cell-lose %
1	109.4^{a} (4.1)	13.8^{a} (0.4)	35.2^{a} (1.1)	246.4^{a} (6.5)	69.0 (0.8)	68.0 (0.8)	55.9^{a} (0.9)	48.8^{a} (1.7)	63.6^{a} (1.2)	76.4^{b} (1.1)
2	90.7^{b} (4.1)	14.4^{a} (0.4)	34.8^{a} (1.1)	193.4^{b} (6.5)	69.7 (0.8)	70.3 (0.8)	62.3^{b} (0.9)	31.9^{c} (1.7)	64.9^{a} (1.2)	82.7^{a} (1.1)
3	85.9^{b} (6.4)	17.0^{b} (0.7)	44.7^{b} (1.8)	182.2^{b} (10.2)	66.4 (1.3)	68.6 (1.3)	65.5^{b} (1.5)	31.2^{c} (2.6)	58.0^{b} (2.0)	76.9^{b} (1.8)
4	82.8^{b} (5.5)	15.2^{ab} (0.6)	34.3^{a} (1.5)	165.1^{b} (8.7)	69.5 (1.1)	70.8 (1.1)	65.3^{b} (1.3)	37.9^{bc} (2.3)	63.4^{a} (1.7)	80.8^{ab} (1.6)
5	90.4^{b} (5.5)	19.3^{c} (0.6)	44.0^{b} (1.5)	183.4^{b} (8.7)	69.8 (1.1)	70.9 (1.1)	65.6^{b} (1.3)	42.2^{ab} (2.3)	64.8^{a} (1.7)	79.7^{ab} (1.6)
Crate mean	83.7* (3.2)	14.8* (0.3)	36.1* (0.9)	194.8 (5.0)	70.4* (0.7)	71.2* (0.6)	62.5 (0.7)	40.7 (1.3)	64.3 (1.0)	80.0 (0.9)
Pen	99.9 (4.6)	17.0 (0.5)	41.1 (1.3)	193.3 (7.3)	67.3 (0.9)	68.2 (0.9)	63.3 (1.0)	36.1 (1.9)	61.6 (1.4)	78.5 (1.3)

abc - when letters differ within columns, the values are significantly different from zero ($P<0.01$).
* - crate/pen effect significant at $P<0.01$. Duncan's New Multiple Range Test.

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Table 6. The effect of temperature on nutrient intake and rates of passage of digesta through the digestive tract.

Experiment	Temperature Treatment	DM intake		N intake		Energy Intake	Mean Retention Time	k_1	k_2	Transit Time	Fecal DM
		g/d	g/w$^{.75}$kg/d	g/d	g/w$^{.75}$kg/d	kJ/w$^{.75}$kg/d	h	1/h	1/h	h	%
1	OUTDOOR	3266	112.8	88.1	3.04	2059	19.9	0.0115	0.0276	6.84	29.3
	INDOOR	2725	101.4	73.5	2.74	1833	22.9	0.0103	0.0278	7.04	33.3
2	OUTDOOR	3241	91.1	94.8	2.66	1627	23.0	0.0164	0.0161	5.56	30.4
	INDOOR	2707	79.5	78.9	2.32	1421	21.7	0.0144	0.0169	6.52	35.5
3	OUTDOOR	3419	82.7	94.9	2.30	1427	27.5	0.0094	0.0145	7.15	29.9
	INDOOR	3149	79.1	87.5	2.20	1384	29.9	0.0103	0.0135	6.63	34.8
4	OUTDOOR	3335	71.8	89.5	1.93	1267	24.0	-	-	-	33.0
	INDOOR	3975	71.3	106.4	1.89	1253	24.1	-	-	-	33.8
5	OUTDOOR	3937	79.6	105.1	2.12	1434	27.8	0.0104	0.0211	6.40	30.7
	INDOOR	5006	87.6	134.1	2.33	1574	28.3	0.0102	0.0154	6.87	31.1
Average	OUTDOOR	3440	87.6	94.5	2.41	1563	24.4	0.0119	0.0198	6.49	30.7*
	INDOOR	3512	83.8	96.1	2.30	1493	25.4	0.0113	0.0184	6.77	33.7

* the temperature average mean values are significantly different ($P<0.001$).

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Table 7. Predicted rate constants (k_1 & k_2) and transit time (TT) to fit the equation of Grovum and Phillips (1973).

Exp.	H	Wapiti ID	k_1 h^{-1}	k_2 h^{-1}	TT h	% var.	S.E.
1	O	1128	0.0782	0.396	6.00	99.7	1.7
	I	1133	0.0537	0.438	6.80	99.8	1.4
	O	1134	0.164	0.159	6.06	99.0	3.2
	I	1135	0.123	0.125	7.98	98.0	5.1
	O	1136	0.120	0.114	3.25	99.3	2.6
	I	1137	0.107	0.272	6.43	98.5	3.9
	O	1138	0.0983	1.00	1.19	89.6	5.7
	I	1139	0.128	1.00	3.72	97.5	2.3
2	O	1128	0.170	0.165	6.09	98.5	4.4
	I	1133	0.210	0.207	5.47	98.7	3.2
	O	1134	0.149	0.150	6.55	96.4	7.5
	I	1135	0.0979	0.0970	7.76	94.1	9.9
	O	1136	0.104	0.0970	6.95	98.2	5.1
	I	1137	0.0765	0.239	6.40	99.4	2.5
	O	1138	0.234	0.234	2.66	99.4	2.0
	I	1139	0.190	0.190	6.47	94.5	7.9
3	O	1128	0.120	0.120	8.04	95.4	8.1
	I	1133	0.0804	0.160	7.63	99.1	3.2
	O	1134	0.107	0.109	6.67	98.9	3.6
	I	1135	0.0693	0.0693	4.84	99.0	3.5
	O	1136	0.0749	0.146	6.72	99.5	2.6
	I	1137	0.118	0.169	7.24	98.9	3.6
	O	1138	0.0758	0.205	7.16	99.0	3.4
	I	1139	0.143	0.141	6.78	98.3	4.8
4	O	1128	0.105	0.105	5.98	99.4	2.4
	O	1138	0.0992	0.0970	2.55	98.7	3.6
5	O	1128	0.0737	0.406	5.14	99.5	2.2
	I	1133	0.124	0.122	6.86	98.8	3.9
	O	1134	0.139	0.138	3.01	99.7	1.6
	O	1136	0.0777	0.176	8.21	98.0	5.0
	I	1137	0.0972	0.0985	7.02	99.2	3.3
	O	1138	0.126	0.126	9.24	99.4	3.0

% var - percent variance accounted; S.E. - standard error of the mean

Exp - experiment; H - temperature treatment; I - IN wapiti; O - OUT wapiti.

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Table 8. The effect of temperature on apparent digestibility.

Experiment	Temperature Treatment	Dry Matter %	Gross Energy %	Nitrogen %	Ether Extr. %	ADF %	NDF %	Hemicellulose %	Dig. E Intake kJ/w·⁷⁵kg/d	Dig. N Intake g/w·⁷⁵kg/d
1	OUTDOOR	68.0	67.0^{jk}	65.6	51.3	43.4^{ab}	61.1	76.4	1378	2.00
	INDOOR	69.0	69.5^{jk}	69.0	53.7	50.9^{bc}	65.2	77.7	1274	1.89
2	OUTDOOR	69.2	67.7^{jk}	69.7	57.8	27.3^{a}	64.6	85.0	1102	1.86
	INDOOR	73.2	71.9^{mnp}	73.1	63.8	39.5^{b}	68.0	83.6	1017	1.70
3	OUTDOOR	70.9	70.9^{kmn}	72.3	69.0	41.6^{b}	64.4	80.6	1004	1.66
	INDOOR	68.4	66.4^{j}	69.0	64.6	36.2^{b}	61.8	80.1	995	1.52
4	OUTDOOR	71.6	70.1^{jkmn}	72.9	64.9	42.0^{b}	63.6	77.9	888	1.40
	INDOOR	75.0	74.1^{np}	75.3	69.4	50.6^{bc}	71.9	86.9	899	1.42
5	OUTDOOR	71.5	70.6^{kmn}	72.0	66.1	44.6^{abc}	65.1	79.0	1013	1.53
	INDOOR	74.8	75.2^{p}	76.0	70.7	53.1^{c}	70.8	83.4	1168	1.78
Average	OUTDOOR	70.3	69.3*	70.5*	61.8	39.8***	63.7**	79.8	1077	1.69
	INDOOR	72.1	71.4	72.5	64.5	46.1	67.6	82.3	1071	1.66

abcde -when letters differ (within columns) the values are significantly different from zero ($P<0.01$)
jkmnp - when letters differ (within columns) the values are significantly different from zero ($P<0.05$)
ADF - acid detergent fiber; NDF - neutral detergent fiber; Ca - calcium; N - nitrogen.
* - temperature average mean values are significantly different from zero ($P<0.05$).
** - temperature average mean values are significantly different from zero ($P<0.025$).
*** - temperature average mean values are significantly different from zero ($P<0.001$).

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Table 9. Nutrient intakes, apparent digestibility of nutrient components and nitrogen (N) retention.

	MONTH				
Parameter	Oct.	Dec.	Feb.	Apr.	Jun.
DM Intake ($g/w^{.75}kg/d$) *	107.1^a (3.4)	85.3^b (3.4)	80.9^b (3.4)	71.5^b (4.4)	83.6^b (4.4)
E Intake ($kJ/w^{.75}kg/d$)	1946^a (59.7)	1524^b (59.7)	1406^b (59.7)	1260^b (77.1)	1504^b (77.1)
N Intake ($g/w^{.75}kg/d$)	2.89^a (0.09)	2.49^b (0.09)	2.25^{bc} (0.09)	1.91^c (0.12)	2.23^{bc} (0.12)
DM Digestibility (%)	68.5^a (0.90)	71.2^{ab} (0.90)	69.7^{ab} (0.90)	73.3^b (1.16)	73.2^b (1.16)
E Digestibility (%)	68.2^a (0.88)	69.8^{ab} (0.88)	68.7^a (0.88)	72.1^{ab} (1.13)	72.9^b (1.13)
N Digestibility (%)	67.3^a (0.85)	71.5^b (0.85)	70.7^{ab} (0.85)	74.1^b (1.09)	74.0^b (1.09)
Fat Digestibility (%)	52.5^a (1.4)	60.8^b (1.4)	66.8^c (1.4)	67.2^c (1.8)	68.4^c (1.8)
ADF Digestibility (%)	47.1^a (1.3)	33.4^b (1.3)	38.9^b (1.3)	46.3^a (1.7)	48.9^a (1.7)
NDF Digestibility (%)	63.1 (1.3)	66.3 (1.3)	63.1 (1.3)	67.7 (1.7)	68.0 (1.7)
Hemicellulose Digestibility (%)	77.0^a (1.5)	84.3^b (1.5)	80.4^{ab} (1.5)	82.4^{ab} (1.9)	81.2^{ab} (1.9)

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abc - when subscripts differ within rows the mean values are significantly different from zero (P<0.01). Duncan's New Multiple Range Test.

* numbers inside brackets are standard errors of the mean.

APPENDIX 4

Table 10. The effect of temperature on water intake, urine output.

Experiment	Temperature treatment	Water intake 1/d	Total water (& feed) intake ml/w$^{.82}$kg/d	Urine output 3 d ml/d	Urine output		Urine & fecal water ml/d
					ml/d	ml/w$^{.82}$kg/d	
1	OUTDOOR	8.9	225.8	3166	3216	81.3	5619
	INDOOR	10.2	273.2	3777	3809	100.3	5276
2	OUTDOOR	8.6	173.5	3784	3727	74.7	6059
	INDOOR	10.4	221.4	4068	4132	85.7	5346
3	OUTDOOR	10.3	177.8	4726	4495	77.3	6844
	INDOOR	11.6	204.6	4926	4743	84.0	6545
4	OUTDOOR	10.3	155.0	4395	4752	72.1	6863
	INDOOR	15.8	201.8	5150	5990	79.6	7952
5	OUTDOOR	12.0	168.5	5382	4709	66.0	7205
	INDOOR	16.7	203.6	5619	5708	72.6	8737
Average	OUTDOOR	10.0*	180.1*	4291	4180	74.3	6518
	INDOOR	12.9	220.9	4708	4876	84.4	6771

* the temperature average mean values are significantly different ($P<0.001$).

APPENDIX 4

Table 11. The effect of temperature on urea-N kinetics.

Experiment	Temperature Treatment	Plasma Urea-N mg %	Urine Urea-N mg %	^{14}C Recovered in Urine %	Urea-N Excreted		Urea-N Recycled		Urea-N Flux	
					g/d	$g/w^{.75}kg/d$	g/d	$g/w^{.75}kg/d$	g/d	$g/w^{.75}kg/d$
1	OUTDOOR	20.0	489	34.4	15.4	0.53	32.0	1.11	47.4	1.64
	INDOOR	20.5	385	33.4	14.0	0.51	33.4	1.25	47.4	1.68
2	OUTDOOR	24.5	580	52.3	21.3	0.59	19.9	0.55	41.2	1.14
	INDOOR	26.0	525	62.1	20.9	0.60	14.2	0.40	35.0	1.01
3	OUTDOOR	25.0	520	53.4	23.4	0.57	21.1	0.52	44.5	1.09
	INDOOR	24.7	410	54.4	19.2	0.47	18.1	0.44	37.3	0.92
4	OUTDOOR	20.7	495	46.2	23.4	0.50	28.3	0.60	52.5	1.12
	INDOOR	22.7	602	44.2	35.5	0.67	43.3	0.86	78.8	1.56
5	OUTDOOR	26.2	522	66.6	24.3	0.49	14.0	0.28	38.4	0.77
	INDOOR	25.2	612	64.7	34.1	0.62	22.6	0.45	56.6	1.11
Average	OUTDOOR	23.3	521	50.6	21.6	0.54	23.0	0.61	44.8	1.15
	INDOOR	23.8	507	51.7	24.7	0.58	26.3	0.68	51.0	1.25

APPENDIX 4

Table 12. Weight (g) of winter hair shed in wapiti.

ELK ID	DATE					
	February 6-13	February 16-23	April 12-21	April 25 to May 4	May 24 to June 3	June 6-16
1128	-	41.0	-	131.4	-	trace
1133	-	94.0	0	-	20.1 (red hair)	-
1134	32.0	-	57.0	145.4	43.5	-
1135	40.0	-	-	-	-	-
1136	8.2	-	124.8	-	36.6 (trace red hair)	-
1137	-	119.6	0	-	31.7 (guard hair-red)	-
1138	-	100.8	-	86.9	-	trace
1139	30.2	-	-	-	-	-

APPENDIX 4

Table 13. Growth rate (kg/d) of wapiti during the time they were on trial.

			WAPITI I.D.							
			OUT WAPITI				IN WAPITI			
Month	Week	Days*	1128	1134	1136	1138	1133	1135	1137	1139
Oct.	1	8	1.025	0.737	0.737	0.800	0.275	0.862	0.512	0.512
	2	9	0.700	0.956	0.656	1.111	0.967	0.656	0.756	0.756
Dec.	1	9	0.455	0.456	0.511	0.600	0.811	0.556	0.655	0.656
	2	10	0.014	0.630	0.460	0.540	0.055	0.500	-0.270	0.590
Feb.	1	8	-0.112	-0.562	-0.237	0.175	-0.287	-0.400	0.112	-0.575
	2	11	0.254	0.245	0.791	0.536	0.373	-	0.582	-
Apr.	1	10	0.320	0.540	-0.270	0.090	0.360	-	0.140	-
	2	14	0	0.669	0.138	0.246	0.700	-	0.277	-
Jun.	1	10	0.730	0.220	-0.450	-0.180	0.500	-	0.550	-
	2	13	0.207	0.561	0.908	0.277	1.010	-	1.015	-

*represents the number of days the rate of gain (kg/d) was calculated.

APPENDIX 4

Table 14. The effect of temperature on urea and creatinine clearances, % C^{14} label recovered and urea-N as a percent of urine nitrogen output.

Experiment	Temperature Treatment	Urea-N clearance 1/d	Urea-N clearance 1/w $^{.75}$kg/d	Creatinine clearance 1/d	Creatinine clearance 1/w $^{.75}$kg/d	% C^{14} recovered %	Urea-N as a % of urine N output %
1	OUTDOOR	77.3	2.67	242.7	8.00	34.4	50.2
	INDOOR	68.1	2.52	250.2	9.11	33.4	53.3
2	OUTDOOR	87.1	2.45	253.5	7.13	52.3	47.6
	INDOOR	81.7	2.44	252.7	7.99	62.1	50.9
3	OUTDOOR	94.6	2.29	287.0	6.97	53.4	48.1
	INDOOR	73.9	1.83	346.5	8.67	54.4	45.2
4	OUTDOOR	112.6	2.43	274.0	5.91	46.2	39.8
	INDOOR	160.1	3.07	377.2	6.94	44.2	53.0
5	OUTDOOR	92.6	1.87	296.2	5.95	66.6	40.3
	INDOOR	138.0	2.52	400.7	6.72	64.7	54.4
Average	OUTDOOR	92.8	2.34	270.7**	6.79*	50.6	45.2
	INDOOR	104.4	2.47	325.5	7.89	51.7	51.4

* temperature average means are significantly different ($P<0.05$).

** temperature aver ge means are significantly different ($P<0.01$).

APPENDIX 5

Table 1. Analysis of variance of blood parameters.

Treatment var.	d.f.	Packed cell Volume % M.S.	P.L.	Hemoglobin g % M.S.	P.L.	Total White Blood Cells M.S. X10^6	mm^3 P.L.	Lymphocytes % M.S.	P.L.	Neutrophils % M.S.	P.L.	Serum Protein g % M.S.	P.L.	Plasma Creatinine mg % M.S.	P.L.
E	4	125.6	<0.005	7.8	<0.005	13.36	<<0.001	720	<0.005	996	<0.001	0.23	ns	0.28	<0.001
T	1	0.3	ns	0.9	ns	1.63	ns	9	ns	36	ns	0.01	ns	0.05	ns
ET	4	19.7	ns	1.3	ns	1.42	ns	152	ns	73	ns	0.03	ns	0.01	ns
U/T	2	24.4	ns	2.5	ns	0.86	ns	154	ns	314	ns	0.39	ns	0.08	<0.025
EU/T	6	17.0	ns	3.4	<0.05	1.69	ns	287	ns	181	ns	0.08	ns	0.03	ns
A/U/T	4	32.6	ns	7.2	<0.005	0.83	ns	273	ns	179	ns	0.49	<0.05	0.03	ns
ERROR		17.2		1.1		0.79		109		106		0.13		0.01	

Treatment Var.	d.f.	Plasma Urea-N mg % M.S.	P.L.	Plasma Calcium mg % M.S.	P.L.	Plasma Phosphorus mg % M.S.	P.L.	Serum Thyroxine µg % M.S.	P.L.	Serum Triiodothyronine ng % M.S.	P.L.	Alkaline Phosphatase U/1 M.S.	P.L.
E	4	41.8	<0.005	9.59	<0.005	4.99	<0.05	4.26	<0.005	4373	<<0.001	3600	<0.001
T	1	2.3	ns	0.70	ns	1.20	ns	0.01	ns	273	ns	18900	<<0.0001
ET	4	2.3	ns	0.66	ns	1.67	ns	1.20	ns	398	ns	1197	<0.025
U/T	2	20.0	ns	1.56	ns	5.12	<0.05	1.26	ns	1514	<0.005	7318	<0.0001
EU/T	6	7.0	ns	1.23	ns	2.82	ns	0.86	ns	503	ns	401	ns
A/U/T	4	1.1	ns	1.49	ns	1.65	ns	1.25	ns	71	ns	2458	<0.005
ERROR	14	6.9		1.43		1.29		0.71		210		286	

Degrees of freedom (d.f.), mean squares (M.S.) and probability levels (P.L.) determined from F-value.

APPENDIX 5

Table 2. Analysis of variance of feed and nutrient intakes.

Treatment Var.	d.f.	DM Intake g/d M.S. $X10^4$	P.L.	Nitrogen Intake g/d M.S.	P.L.	DM Intake $g/w^{.75}kg/d$ M.S.	P.L.	Gross Energy Intake $KJ/w^{.75}kg/d$ M.S. $X10^3$	P.L.	Nitrogen Intake $g/w^{.75}kg/d$ M.S.	P.L.	Digestible Energy Intake $KJ/w^{.75}kg/d$ M.S. $X10^3$	P.L.	Digestible Nitrogen Intake $g/w^{.75}kg/d$ M.S.	P.L.
E	4	209.7	<<0.001	1228	<0.005	1177	<<0.001	457	<<0.001	0.85	<<0.001	176	<0.001	0.26	<0.01
T	1	4.0	ns	19	ns	109	ns	37	ns	0.10	ns	0	ns	0.01	ns
ET	4	73.3	<0.025	551	<0.025	97	ns	34	ns	0.07	ns	15	ns	0.04	ns
U/T	2	56.0	ns	408	ns	100	ns	42	ns	0.102	ns	28	ns	0.06	ns
EU/T	6	2.9	ns	38	ns	33	ns	9	ns	0.03	ns	6	ns	0.02	ns
A/U/T	4	43.9	ns	339	ns	148	ns	42	ns	0.12	ns	36	ns	0.06	ns
ERROR	14	17.8		133		91		285		0.172		21.1		0.07	

Treatment Var.	d.f.	Water Intake ml/d M.S. $X10^6$	P.L.	Total Water Intake $ml/w^{.82}kg/d$ M.S.	P.L.
E	4	25.5	<0.001	5624	<0.010
T	1	63.6	<<0.001	12456	<<0.001
ET	4	5.6	ns	167	ns
U/T	2	22.1	<0.01	563	ns
EU/T	6	2.6	ns	700	ns
A/U/T	4	7.8	ns	854	ns
ERROR	14	2.9		1040	

Treatment Var.	d.f.	DM intake g/d M.S.	P.L.	DM intake $g/w^{.75}kg/d$ M.S.	P.L.	Calcium Intake g/d M.S.	P.L.	Phosphorous Intake g/d M.S.	P.L.	Water Intake ml/d M.S. $X10^4$	P.L.	Total Water Intake (& feed) $ml/w^{.82}kg/d$ M.S.	P.L.	% DM Feces M.S.	P.L.
E	4	318	<<0.001	1287	<0.005	252	<0.001	49.4	<0.001	2614	<0.001	11320	<0.001	16.3	ns
W/E	5	31	ns	179	ns	55	<0.05	7.1	ns	83	ns	168	ns	8.4	ns
T	1	60	ns	456	ns	79	ns	12.9	ns	1156	<0.025	5419	<0.01	4224	<0.001
TE	4	19	ns	145	ns	23	ns	3.7	ns	179	ns	1026	ns	10.9	ns
TW	5	11	ns	410	ns	9	ns	2.4	ns	194	ns	428	ns	13.3	ns
C	1	183	<0.001	2096	<0.01	202	<0.005	37.4	<0.005	33	ns	17	ns	4.3	ns
CE	4	18	ns	340	ns	16	ns	3.5	ns	222	ns	415	ns	7.3	ns
CT	1	1	ns	4	ns	0	ns	0.4	ns	0	ns	201	ns	57.8	<0.01
U/T	2	22	ns	206	ns	31	ns	4.6	ns	1326	<0.005	343	ns	52.4	<0.005
EU/T	6	18	ns	162	ns	22	ns	3.6	ns	389	ns	913	ns	42	ns
A/U/T	4	64	ns	211	ns	80	<0.025	13.6	<0.01	840	<0.01	1815	<0.05	103	ns
ERROR	32	16		266		20		3.3		189		667		6.7	

Degrees of freedom (d.f.), mean squares (M.S.) and probability levels(P.L.) determined from F-values.

APPENDIX 5

Table 3. Analysis of variance of the apparent digestibility determinations and mean retention time (MRT) of ^{103}Ru in the digestive tract.

Treatment		Dry matter		Energy		Nitrogen		Ether Extract		Acid Detergent Fiber		Neutral Detergent Fiber		Hemicellulose		Mean Retention Time h	
var.	d.f.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.
E	4	26.5	<0.025	23.8	<0.025	47.9	<0.001	303.3	<<0.001	290	<<0.001	35.2	ns	56.2	<0.05	79.4	<0.025
T	1	25.3	ns	34.5	<0.05	28.5	<0.05	51.6	ns	294	<<0.001	108.8	<0.025	48.4	ns	7.0	ns
ET	4	13.3	ns	26.5	<0.025	17.4	ns	32.2	ns	88	<0.005	25.8	ns	24.0	ns	6.0	ns
U/T	2	5.4	ns	5.4	ns	12.1	ns	38.7	ns	35	ns	6.2	ns	6.8	ns	17.1	ns
EU/T	6	6.3	ns	9.0	ns	8.0	ns	30.6	ns	33	ns	5.2	ns	8.1	ns	33.1	ns
A/U/T	4	0.7	ns	3.3	ns	5.1	ns	11.4	ns	17	ns	3.6	ns	25.3	ns	84.2	<0.025
ERROR	14	9.7		11.0		5.8		15.6		14		14.5		17.2		17.9	

Treatment		Dry Matter %		Nitrogen %		Fat %		ADF %		NDF %		Hemicellulose %		Ca %		P %	
Var	d.f.	M.S. X10^4	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.
E	4	18.6	ns	22.4	ns	192	<0.001	732	<0.001	70.3	<0.05	97.6	<0.005	999	<0.001	801	<0.001
W/E	5	11.3	ns	14.1	ns	33	ns	54	ns	13.2	ns	17.9	ns	43	ns	241	<0.025
T	1	12.8	ns	10.9	ns	56	ns	58	ns	18.0	ns	6.5	ns	322	ns	10	ns
TE	4	12.5	ns	16.2	ns	26	ns	162	<0.025	17.1	ns	4.8	ns	365	<0.01	90	ns
TW	5	7.0	ns	12.7	ns	18	ns	29	ns	19.4	ns	26.9	ns	56	ns	36	ns
C	1	77.5	<0.025	71.0	<0.025	5	ns	166	ns	58.0	ns	17.8	ns	4	ns	546	<0.025
CE	4	19.0	ns	17.8	ns	39	<0.05	108	ns	43.6	ns	31.5	ns	57	ns	109	ns
CT	1	5.0	ns	0.6	ns	9	ns	0	ns	0.9	ns	1.0	ns	2	ns	103	ns
U/T	2	18.5	ns	41.8	<0.05	127	<0.005	55	ns	21.8	ns	13.4	ns	77	ns	604	<0.005
EU/T	6	7.7	ns	12.2	ns	29	ns	33	ns	17.1	ns	17.5	ns	52	ns	44	ns
A/U/T	4	3.3	ns	3.1	ns	19	ns	18	ns	20.6	ns	48.2	ns	91	ns	399	<0.005
ERROR	32	11.5		11.1		14		45		24.7		21.1		81		73	

Degrees of freedom (d.f.), mean squares (M.S.) and probability levels (P.L.) determined from F-values.

APPENDIX 5

Table 4. Analysis of variance of parameters related to the kinetics of retention time of digesta and of urea-N; and the analysis of variance of urine output and nitrogen metabolism.

Treatment		Urea-N in Urine mg %		Urea-N Excretion g/d		Urea-N Recycled g/d		Urea-N Flux g/d		Urea-N Excretion $g/w^{.75}kg/d$		Urea-N Recycled $g/w^{.75}kg/d$		Urea-N Flux $g/w^{.75}kg/d$	
var.	d.f.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.
E	4	23117	ns	225	<0.005	511	<0.025	643	ns	0.009	ns	0.79	<0.01	0.64	<0.05
T	1	1650	ns	74	ns	80	ns	292	ns	0.011	ns	0.03	ns	0.07	ns
ET	4	15101	ns	72	ns	100	ns	313	ns	0.017	ns	0.05	ns	0.10	ns
U/T	2	13439	ns	55	ns	656	<0.025	1087	<0.05	0.005	ns	0.29	ns	0.45	ns
EU/T	6	12024	ns	22	ns	120	ns	191	ns	0.012	ns	0.06	ns	0.12	ns
A/U/T	4	16169	ns	21	ns	129	ns	230	ns	0.008	ns	0.08	ns	0.09	ns
ERROR	14	9635		31.2		129		273		0.020		0.13		0.2	

Treatment		k_1 1/h		k_2 1/h		Transit Time h	
var.	d.f.	M.S. X10⁻⁴	P.L.	M.S. X10⁻⁴	P.L.	M.S.	P.L.
E	3	0.5	<0.05	2.9	<0.025	1.34	ns
T	1	0	ns	0.1	ns	0.53	ns
ET	3	0	ns	0.1	ns	0.75	ns
U/T	2	0.1	ns	2.6	<0.05	0.07	ns
EU/T	5	0.2	ns	0.2	ns	2.82	ns
A/U/T	4	0.3	ns	0.7	ns	0.55	ns
ERROR	11	0.2		0.6		2.87	

Treatment		N in urine g/d		N retained g/d		Urine Flow ml/d		Urine Flow (3 day collection) ml/d		Urine and Fecal water ml/d		Urine flow $ml/w^{.82}kg/d$		Urea-N as a % of urine N output in g/d		% label C^{14} recovered	
Var.	d.f.	M.S.	P.L.	M.S.	P.L.	M.S. X10³	P.L.	M.S. X10⁶	P.L.	M.S. X10³	P.L.	M.S.	P.L.	M.S.	P.L.	M.S.	P.L.
E	4	1473	<<0.001	481	<<0.001	3844	<0.025	4.06	<0.05	6796	<0.025	377	ns	35.8	ns	991	<<0.001
T	1	0	ns	95	ns	3637	ns	1.31	ns	482	ns	772	ns	284.4	ns	10	ns
ET	4	112	<0.05	239	<0.005	237	ns	0.10	ns	1326	ns	50	ns	74.2	ns	44	ns
U/T	2	38	ns	25	ns	5310	<0.025	4.16	<0.05	9020	<0.025	528	ns	15.3	ns	297	<0.005
EU/T	6	59	ns	72	ns	230	ns	0.82	ns	225	ns	85	ns	136.1	ns	103	<0.05
A/U/T	4	106	<0.05	38	ns	968	ns	1.58	ns	1232	ns	580	ns	176.6	ns	80	ns
ERROR	14	32		35		917		1.10		1449		357		78.6		33	

Degrees of freedom (d.f.), mean squares (M.S.) and probability levels (P.L.) determined from F-values.

APPENDIX 5

Table 5. Analysis of variance of the rate of body weight gain in growing wapiti.

Treatment var.	d.f.	Rate of gain kg/d M.S.	P.L.
E	4	0.519	<0.005
W/E	5	0.334	<0.005
T	1	0.112	ns
ET	4	0.186	ns
TW	5	0.049	ns
C	1	0.353	<0.05
CE	4	0.109	ns
CT	1	0	ns
U/T	2	0.006	ns
EU/T	6	0.036	ns
A/U/T	4	0.020	ns
ERROR	32	0.730	

Degrees of freedom (d.f.), mean square (M.S.) and probability levels (P.L.) determined from F-values.

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